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NOMENCLATURAL UNITS AND TROPICAL AMERICAN MIOCENE SPECIES OF THE GASTROPOD FAMILY CANCELLARIIDAE

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ABSTRACT—Many undescribed species of Cancellariidae are known to occur in the Miocene strata of tropical America. The majority of these, and of the numerous described species, cannot satisfactorily be included in existing classificatory units. In order to place the cancellariids in their proper systematic position, many Tertiary species yet undetected must be found and analyzed and their phylogenetic sequences worked out. This paper presents, as a basis for analytical studies, a list of the available supra-specific categories, a key to identification of the principal subgenera, a list of recorded tropical American Miocene species, and descriptions of six new Ecuadorean Miocene species. Two new subgeneric names are proposed: *Bivetiella* for *Bivetia* auctt., and *Hertleinia*.

INTRODUCTION

The family Cancellariidae is a well-defined natural group, constituting those genera with more or less cancellate sculpture, an oblique protoconch of two or three barren whorls and two or three raised plaits on the columella. The multiplicity of species within the family has caused the proposal of extremely varied schemes for their classification and a correspondingly large number of supra-specific nomenclatural categories. None of the arrangements presented to date has satisfied all current researchers, and the need for new data on phylogenetic series and for a comprehensive revision of the family is evident. The Miocene expansion of the Cancellariidae after their comparatively obscure past has been noted.[1] Recent paleontological studies in northern South America have uncovered scores of new species of Cancellariidae in the Miocene strata. The previously undescribed Ecuadorean Miocene yielded approximately 30 species, of which six are herein recorded. Mr. Frank V. Stevenson, paleontologist of the Tropical Oil Co., reports as many as 16 species from a single formation in Colombia.[2] Forty-four tropical American Miocene species are already recorded in the literature, and are catalogued in this paper (p. 459 et seq.). Since the Miocene strata are closely related to the petroleum resources of tropical America, a successful biostratigraphical study of the Cancellariidae would produce economic as well as academic results.

The present paper is not an attempt to revise the Cancellariidae. A comprehensive

[1] E.g., Davies, A. M., 1935, Tertiary Faunas, p. 307.

[2] Personal communication, June 12, 1948.

revision or reorganization of the family, in the writer's opinion, should not be attempted until analytical data on many lines of descent, from past ages to Recent, are available. The present paper is intended as a basis for future analytical work. It consists of a partially annotated catalogue of the available supraspecific names, notes on methods of analyzing and classifying some groups of cancellariids, a key to the principal subgenera, a catalogue of the described tropical American Miocene species, and the description of six new Ecuadorean Miocene species. Two new subgeneric names are proposed: *Bivetiella* for *Bivetia* auctt., and *Hertleinia*.

ACKNOWLEDGMENTS

The present study was made at Stanford University, California. The excellent collection of Recent shells, the extensive conchological library, and the kind cooperation of the staff of the School of Mineral Sciences have greatly aided the work. Special thanks are due to Dr. A. Myra Keen, Curator of the Stanford Paleontology and Conchology collections, for helpful, authoritative assistance on problems of nomenclature and identification. The International Petroleum Company, Ltd., Toronto, Canada was generous in granting the use of its extensive collections of Ecuadorean Miocene fossils, and in giving permission to publish.

CLASSIFICATION OF THE CANCELLARIIDAE

No satisfactory classification of the Cancellariidae exists. The difficulties inherent in classifying the family are proved by the multiplicity of schemes by which the proposed generic and subgeneric units have been grouped. The failure of these classificatory schemes and the root of the trouble are that the phylogenetic relations—the true basis of systematics—have not been resolved. The impossibility of grouping the many Recent species correctly without regard to their ancestry is becoming evident. The difficulty of finding the ancestors of Recent species among the small percentage of formerly existing species that has been described is also apparent. The ever-increasing numbers of new tropical American Miocene species in the literature point out the inadequacy of our knowledge of the family as a whole.

H. and A. Adams (1858, The genera of Recent Mollusca, pp. 275–278) arranged the Cancellariidae as follows:

Genus	*Cancellaria*
Subgenera	*Cancellaria*
	Trigonostoma
	Aphera
	Euclia
	Merica
	Narona
	Massyla
Genus	*Admete*

Crosse (1861, Jour. Conchyl., p. 220) deplored the subdivision of the naturally formed genus *Cancellaria* into subgenera, and grouped all species into three admittedly artificial groups based on the shape of the shell: trigonostomes, purpuriformes, and mitriformes. Crosse's arrangement, artificial though it be, has some value from a practical standpoint. Tryon (1885, Manual of Conchology, vol. 7, pp. 65–98) placed all 100 of the species he recognized in one genus *Cancellaria*, with subgenera *Cancellaria* and *Admete*. Jousseaume (1887) placed a similar number of species in 22 different genera. Cossmann (1899, Essais de Paleo. Comp., vol. 3, pp. 1–41) presented the most elaborate subdivision of the Cancellariidae, grouping them in the subfamilies Cancellinae, Trigonostominae and Admetinae, with genera, subgenera, and sections grouped thereunder. Thiele (1929, Handbuch der systematischen Weichtierkunde, pp. 351–353) used the genera *Cancellaria* and *Admete*, and placed under *Cancellaria* the subgenera *Cancellaria*, *Trigonostoma*, *Narona* and *Aphera*, with various sections under each.

More recently, A. A. Olsson, dealing with tropical American Tertiary species, has used eight subgeneric names, each applied in careful accordance with the concept of type species. The recent classification by A. M. Strong (1945, Proc. Conch. Club California, vol. 1, pt. 2, no. 49, pp. 2–15) is the result of extensive research, and is a satisfactory grouping of the Recent West Coast species according to our present knowledge. His arrangement is as follows:

Genus	*Cancellaria*
Subgenera	*Cancellaria*
	Euclia
	Narona
Genera	*Bivetopsia*
	Trigonostoma
	Massyla
Subgenera	*Massyla*
	Aphera
Genus	*Admete*

The writer believes that a systematic classification of the Cancellariidae must depend not only on comparative morphology, but also on phylogeny—the tracing of lineages. The startling number of Miocene species now being discovered lends emphasis to the thesis that we must find and analyze a large, unknown number of fossil species before we can place any species in its proper systematic relation to the rest of the family.[3] Until these lineages are traced out and their morphologic qualities analyzed, no classificatory scheme can be completely convincing. The statement of this procedure implies that the major portion of discovery and study on the Cancellariidae remains to be done.

The principle of summation of characters is the main criterion in a study on comparative morphology. No single morphologic feature may be disregarded; and conversely, no single feature may be used as a unique criterion for classification. In the cancellariids, the protoconch, sculpture of first spire whorl, shape of body whorl, and curvature of columella are important features to which sufficient attention has not always been paid. The shape and sculpture of the earliest spire whorls in particular seem to be of primary importance because, to a limited extent, they reflect the biologists' axiom that "ontogeny repeats phylogeny." The shape of the body whorl is important because it reflects the shape of the animal itself. Study of the living animal should be called upon to interpret the meaning and importance of the morphologic features: such biological studies on the Cancellariidae are few.[4]

Three general groups of cancellariids have been recognized by most conchologists:

FIG. 1—Camera lucida drawings of apices and early spire whorls of some Cancellariidae. *a*, *Admete couthouyi* Jay, Recent, west coast of Canada. *b*, *Cancellaria* (*Cancellaria*) *reticulata* Linné, Recent, east coast of Panama; type of *Cancellaria*. *c*. *Trigonostoma rigida* Sowerby, Recent, Peru.

Cancellaria, *Trigonostoma*, and *Admete*. According to the summation of characters, the type species of the groups are morphologically distinct. Analysis of their protoconchs and early whorls shows genuine differences at early stages of growth (fig. 1, a, b, c). *Admete* is further distinguished by its geographic distribution, for it is rarely found in warm waters. *Trigonostoma* is not abundant in the fossil state, only five species from tropical American Miocene strata being on record. Of the generalized group called *Cancellaria*, species closely related to *C. reticulata*, type of the genus, are commonest in the Miocene strata. Species of the restricted subgenus *Bivetiella* are often found in strata as old as Lower Miocene. The subgenus *Hertleinia* is at present known only as Quaternary and Lower Miocene.

SUPRA-SPECIFIC NOMENCLATURAL UNITS OF THE CANCELLARIIDAE

The following partly annotated list is arranged alphabetically. Valid names are in capital letters; invalid names are in small

[3] For a discussion of classificatory criteria, see Frizzell, D. L., 1936, Preliminary reclassification of veneracean pelecypods, Bull. Mus. Roy. Hist. Nat. Belg., vol. 12, no. 34, pp. 3–7.

[4] See Tryon, *op cit.*, pp. 67, 71, 84.

type; supra-generic names are not included. References not seen by the writer are indicated by an asterisk.

ADMETE Möller, 1842. Index Moll. Groenl., p. 15. Proposed as a genus. Type (by monotypy), *Admete crispa* Möller, Recent, northern Atlantic. According to Grant and Gale (1931, p. 622), *A. crispa* is "a minor variety of *Cancellaria couthouyi* Jay." *A. couthouyi* is circumboreal in Recent seas. The group of *Admete*, s. l., is geographically as well as morphologically distinct from *Cancellaria* and *Trigonostoma*.

ADMETULA Cossmann, 1889. Ann. Soc. Roy. Malac. Belg., vol. 24, p. 224. Proposed as a section of genus *Cancellaria*. Type (by original designation), *Cancellaria evulsa* (Solander), Eocene (?) of England. In 1899 Cossmann stated that the principal difference between *Admetula* and *Bonellitia* was not constant and synonymized *Admetula* to the prior *Bonellitia*.

ANAPEPTA Finlay, 1930. Trans. N. Z. Inst., vol. 61, p. 240. Proposed as a subgenus of *Inglisella* Finlay. Type (by original designation), *Inglisella* (*Anapepta*) *septentrionalis* Finlay, Recent, New Zealand.

ANEURYSTOMA Cossmann, 1899. Essais de Paleo. comp., vol. 3, p. 23, Proposed as a subgenus of *Sveltia* Jousseaume as used by Cossmann. Type (by original designation), *Cancellaria dufouri* Grateloup, Miocene. Occurrence: Eocene and Miocene strata of Europe.

ANTEPEPTA Finlay and Marwick, 1937. N. Z. Geol. Surv., Paleo. Bull. no. 15, p. 83. Proposed as a genus. Type (by original designation), *Antepepta* nasuta Finlay and Marwick, Cretaceous of New Zealand. *Antepepta* appears to be similar to *Pristimerica*.

APHERA H. and A. Adams, 1858. The genera of Recent Mollusca, vol. 1, p. 277. Proposed as a subgenus of *Cancellaria*. Type (by monotypy), *Cancellaria tessellata* Sby., Recent, west coast of tropical America.

ARIZELOSTOMA Iredale, 1936. Rec. Australian Mus., vol. 19, no. 5, p. 318. Proposed as a genus. Type (by original designation), *A. laseroni* Iredale, Recent, Australia.

BABYLONELLA Conrad, 1865. Amer. Jour. of Conch., vol. 1, p. 32. Proposed as a subgenus of *Cancellaria*. Type (by subsequent designation, Cossman, 1899), *Cancellaria elevata* Lea, Eocene of Alabama.

BENTHOBIA Dall, 1889. Bull. Mus. Comp. Zool. Harvard, vol. 18, p. 131. Proposed as a genus. Type (by original designation) *Benthobia tryoni* Dall, living in 730 fathoms off Cape Fear, North Carolina. Dall distinguishes *Benthobia* from *Admete* by the absence of columellar folds. Cossmann (1899, p. 6) states that many *Admetes* show a tendency to lose their columellar folds, and presumes therefore that *Benthobia* is hardly a section distinct from *Admete*. Thiele (1929, p. 353) notes that *Benthobia* is "little different" from *Admete*.

BIVETIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, fasc. 14, p. 163 (with fig. 1). Type (by monotypy), *Bivetia mariae* Jousseaume, sp. nov., Recent, habitat unknown. Jousseaume described *Bivetia mariae* in fascicle 14, p. 163 of "Le Naturaliste," thus making *B. mariae* the type of *Bivetia* by monotypy. In fascicle 16, p. 193 of the same journal, Jousseaume proposed *Bivetia* with *Voluta cancellata* Linné as type. This latter designation is, of course, not valid since the other has priority. *Bivetia mariae* Jousseaume probably prescribes to the concept of "Le Bivet" of Adanson, described from examples of *C. cancellata* and *C. similis*.[5] Jousseaume considered it to belong to that unit; and, more recently, E. Fischer-Piette[6] so considers it. Unfortunately, *B. mariae* is represented only by a unique specimen in the Muséum National d'Histoire Naturelle in Paris; its habitat is unknown and, according to Professor Fischer-Piette, the first sculptured whorls are " . . . assez usés mais on se rend compte cependant que leur sculpture est toute de suite semblable à ce qu'elle est plus loin, c'est-à-dire très semblable à celle de *C. cancellata*."

In order to provide a surer basis for the unit "Le Bivet" than the unique specimen first described by Jousseaume, the new name *Bivetiella* (q.v.) is herein proposed. Should well-preserved specimens of *B. mariae* be discovered and found to have the same characters as *Bivetiella*, the latter name could be synonymized.

BIVETIELLA Marks, subg. nov.

"Le Bivet" Adanson, 1757, p. 163, pl. 8, fig. 16. *Bivetia* auctt. (not *Bivetia* Jousseaume 1887, p. 163).

Type species: *Cancellaria similis* Sowerby, Recent, west coast of Africa. The principal distinguishing features of the subgenus *Bivetiella* are: shape stout, with a broad body whorl; earliest spire whorl evenly convex with regular cancellate sculpture; adult sculpture cancellate; later whorls slightly carinate; outer lip internally lirate, strongly everted, and with a sinus or "stromboid notch"; anterior extremity with a short canal and a moderately deep notch; posterior notch shallow but distinct.

Bivetiella is here proposed to replace *Bivetia* auctt., thus making available a term for the unit proposed by Adanson as "Le Bivet" (loc. cit.). According to Fischer-Piette (1942, "Les mollusques d'Adanson," Jour. Conchyl., ser. 4, vol. 85, p. 219), Adanson described his "Le Bivet" with three specimens of *Cancellaria cancellata* (Linné) and one of *C. similis* Sowerby before him, and figured the *C. similis*. Adanson's work, of course, is not accepted, because it is pre-Linnean. *Bivetia* (q.v.) dates from Jousseaume, 1887, with type, by monotypy, *B. mariae* Jousseaume. As noted by other authors, as well as by Adanson, *C. similis* is fundamentally like *C. cancellata*. The unit is at present represented on the west coast of America by *C. pulchra* Sowerby, and in the fossil state by many species, including *C. epistomifera* Guppy, Miocene of Santo Domingo and Panama, and *C. santiagensis* Marks and *C. frizzelli* Marks, Miocene of Ecuador.

[5] Fischer-Piette, 1942, Jour. Conchyl, ser. 4, vol. 85, p. 219.

[6] Personal communication, March 18, 1948.

BIVETOPSIA Jousseaume, 1887. Le Naturaliste, s. 2, vol. 1, fasc. 16, p. 193. Proposed as a genus. Type (by subsequent designation, Cossmann 1899, p. 9), *Cancellaria chrysostoma* Sowerby, Recent, west coast of northern South America and Panama. (*Bivetopsis* Jousseaume, 1887, an emendation of *Bivetopsia* proposed by Cossmann, 1889, p. 9.)

BONELLITIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, no. 19, p. 223. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Cancellaria bonellii* Bellardi, Pliocene of Italy. Cossmann uses *Bonellitia* as a section of the genus *Admete*.

BROCCHINIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, no. 19, p. 221. Proposed as a genus. Type (by monotypy implied in original description), *Cancellaria mitraeformis* Brocchi, Pliocene of Italy.

CALCARATA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, fasc. 18, p. 214. Proposed as a genus. Type (by original designation), *Cancellaria calcarata* Brocchi, Pliocene of Italy. Cossmann uses *Calcarata* as a section of his genus *Sveltia* (q.v.).

CANCELLAPHERA Iredale, 1930. *Mem. Queensland Mus., vol. 10, pt. 1, p. 80. Proposed as a genus. Type (by original designation), *Cancellaphera amasia* Iredale, Recent.

CANCELLARIA Lamarck, 1799. *Mem. Soc. Hist. Nat. Paris, vol. 1, p. 71. Proposed as a genus. Type (by monotypy), *Voluta reticulata* Linné, Recent, Florida and the West Indies.

CANCELRANA Palmer, 1937. Bull. Amer. Paleontology, vol. 7, p. 455. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Pleurotoma* (*Taranis*) *finexa* Harris, Claiborne Eocene, United States.

Palmer notes closest affinity of the genus as probably *Plesiocerithium* Cossman 1889. The only species is the type species.

CAVEOLA Stephenson, 1941. The larger invertebrate fossils of the Navarro group of Texas, Univ. of Texas Publ., no. 4101, p. 363. Proposed as a genus. Type (by original designation), *Cancellaria acuta* Wade, Cretaceous of Tennessee and Texas.

> The features which serve to differentiate *Caveola* from *Cancellaria* are its exceptionally high spire, the presence of varices on the whorls, the absence of both an anterior fasciole and an umbilical fissure, and the absence of a spiral sulcus at the base of the body whorl. (Stephenson, 1941, p. 363.)

CHARCOLLERIA Olsson, 1942. Bull. Amer. Paleontology, vol. 27, no. 106, p. 61. Proposed as a subgenus of *Cancellaria* Lamarck. Type (by original designation), *Cancellaria* (*Charcolleria*) *perdiciana* Olsson, Miocene of Colombia.

COPTOSTOMA Cossmann, 1899. Essais de Paleo. Comp., vol. 3, p. 34. Proposed as a section of the genus *Admete*. Type (by original designation), *Cancellaria quadrata* Sowerby, Eocene.

COPTOSTOMELLA Finlay and Marwick, 1937. New Zealand Geol. Surv. Pal. Bull. no. 15, p. 83. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Coptostomella pupa* Finlay and Marwick, Cretaceous of New Zealand. The relationship of *Coptostomella* to *Coptostoma* Cossmann is noted.

CRAWFORDINA Dall, 1918. Proc. Biol. Soc. Washington, vol. 31, p. 138. Proposed as a section of the genus *Cancellaria*, subgenus *Progabbia*. Type (by original designation), *Cancellaria crawfordiana* Dall, Recent, west coast of North America.

EUCLIA H. and A. Adams, 1848. The Genera of Recent Mollusca, vol. 1, p. 277. Proposed as a subgenus of *Cancellaria*. Type (by subsequent designation, Cossmann, 1899), *Cancellaria cassidiformis* Sby. As noted by Olsson, 1932, H. and A. Adams listed four species: *bulbulus* Sby. *cassidiformis* Sby., *pyrum* Ad. and Reeve, and *solida* Sby. Cossmann selected *cassidiformis* Sby. as type, thereby leaving the group typified by *C. solida* (cited by other authors as the type of *Euclia*) without a subgeneric name. Olsson corrected this situation by erecting *Pyruclia* (q.v.) with *C. solida* Sby. as type.

EXECHOPTYCHIA Cossmann, 1903. Essais de Paleo. Comp., pt. 5, pp. 189–190. Proposed as a genus. Type (by original designation), *Cancellaria conradiana* Dall, Pliocene, Florida. Cossmann considered *Exechoptychia* as a genus intermediate between *Cancellaria* and his *Bivetia* (=*Bivetiella*). Woodring (1928, p. 218) stated that it is a synonym of *Cancellaria* s.s.

GULIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, fasc. 16, p. 193. Proposed as a genus. Type (by subsequent designation, Cossmann 1899, p. 27), *Cancellaria acutangula*. Cossmann synonymizes *Gulia* to *Ventrilia*, saying that *Gulia* was created only for the fossil representatives of *Ventrilia*, which is represented principally by living species.

HERTLEINIA Marks, subg. nov.

Type: *Cancellaria mitriformis* Sowerby, 1832, Recent, west coast of tropical America.

Description of the subgenus (based on *Cancellaria mitriformis* Sowerby, *C. uniplicata* Sowerby, and *C. angosturana* Marks): shape mitriform; protoconch of three rapidly increasing, bare whorls, oblique to axis of shell; early sculpture of about eleven strong axial ribs per whorl, crossed near the posterior suture by a single strong spiral band; adult sculpture cancellate with one predominant posterior spiral band; aperture elongate, with a short, recurved anterior canal, moderately deep notch, and barely impressed posterior notch; columella with two low folds; outer lip slightly thickened away from the margin, crenate, internally lirate, with distinct sinus; siphonal fasciole low, merging with posterior columellar plait.

The known stratigraphic range of *Hertleinia* is lower Miocene to Recent. The lower Miocene *C.* (*Hertleinia*) *angosturana* is slightly smaller than the Recent *C. mitriformis* and *C. uniplicata*, and has more secondary sculpture on the columella, heavier columellar folds, and a slightly weaker posterior spiral band on the adult whorls.

C. mitriformis, the type of *Hertleinia*, has been placed in *Narona* by some authors. *Narona* (type *C. clavatula* Sowerby) may be distinguished by

its swollen axial ribs, bicarinate early spire sculpture, and posteriorly enlarged aperture.

The new subgenus is named for Dr. Leo G. Hertlein, of the California Academy of Sciences.

Heteroeuclia Rovereto, 1899. Soc. ligurist. di sci. e let., Pavia, atti, vol. 10, p. 103. Rovereto considers *Euclia* H. and A. Adams to be preoccupied by *Euclea* Hübner 1816 ("lepidottero") and mentions also *Euclea* Newnan 1842 ("coleotero"). Here therefore proposes *Heteroeuclia* for *Euclia*, but designates no type.

INGLISELLA Finlay, 1924. Trans. New Zealand Inst., vol. 55, p. 513. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Ptychatractus pukeuriensis* Suter, Miocene of New Zealand. Finlay (1926, p. 428 and 1930, p. 241) considers *Microsveltia* Iredale 1925 to be an absolute synonym of *Inglisella*.

JUNGHUHNIA Martin, 1931. *Wetens. Meded. Mijnb. Weltevreden, vol. 18, p. 11, fig. Proposed as a subgenus of *Trigonostoma*. Type (? by original designation), *Trigonostoma* (*Junghuhnia*) *ficus* Martin, sp. nov., Eocene of Java.

MAORIVETIA Finlay, 1924. Trans. New Zealand Inst., vol. 55, p. 513. Proposed as a genus of the family *Cancellariidae*. Type (by original designation) *Turbinella brevirostris* Hutton, Miocene of New Zealand. Finlay compares *Maorivetia* with *Uxia*, *Aphera* and *Bivetia*.

MASSYLA H. and A. Adams, 1858. The genera of Recent Mollusca, vol. 1, p. 278. Proposed as a subgenus of *Cancellaria*. Type (by monotypy), *Cancellaria corrugata* Hinds, Recent, west coast of tropical America (*Masslya* in Cossmann, a misspelling of *Massyla* H. and A. Adams).

MERICA H. and A. Adams, 1858. The genera of Recent Mollusca, vol. 1, p. 277. Proposed as a subgenus of *Cancellaria*. Type (by subsequent designation, Cossmann, 1899), *Cancellaria melanostoma* Sby. (= *C. asperella* Lam. fide Cossmann), Recent, western Pacific.

MERICELLA Thiele, 1929. Handb. der Syst. Weicht., p. 353. Proposed as a section of the genus *Cancellaria*, subgenus *Narona*. Type (by monotypy), *Cancellaria jucunda* Thiele.

MICROCANCILLA Dall, 1924. Bull. Biol. Soc. Washington, vol. 27, p. 87. Proposed as a section of *Admete* Möller. Type (by original designation), *Admete microscopica* Dall.

MICROSVELTIA Iredale, 1925. *Records Australian Mus., vol. 14, p. 265. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Microsveltia recessa* Iredale, sp. nov., Recent. Finlay, 1930, considers *Microsveltia* to be an absolute synonym of *Inglisella* Finlay (q.v.).

NARONA H. and A. Adams, 1858. The genera of Recent Mollusca, vol. 1, p. 277. Proposed as a subgenus of *Cancellaria*. Type (by subsequent designation, Cossmann, 1899), *Cancellaria clavatula* Sby., Recent, west coast of Central America.

NEVIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, no. 19, p. 222. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Cancellaria spirata* Lamarck. Cossmann synonymizes *Nevia* to *Merica*.

OAMARUIA Finlay, 1924. Trans. and Proc. N. Z. Inst., vol. 55, p. 514. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Admete suteri* Marshall and Murdock, Miocene of New Zealand.

OVILIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, fasc. 16, p. 193. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Ovilia doliolaris* (Basterot), fossil. Cossmann (1899, pp. 4 and 28) used *Ovilia* as a section of the genus *Trigonostoma*.

PEPTA Iredale, 1925. Rec. Australian Mus., vol. 14, p. 265. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Admete stricta* Hedley, Recent.

PLESIOCERITHIUM Cossmann, 1889. Ann. Soc. Roy. Malac. Belg., vol. 24, p. 228. Proposed as a genus. Type (by original designation), *Cancellaria magloirei* Mellev., Eocene, Paris Basin. In 1899, Cossmann placed *Plesiocerithium* in the subfamily *Admetinae*.

PRISTIMERICA Finlay and Marwick, 1937. New Zealand Geol. Surv. Pal. Bull. no. 15, p. 82. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *P. dolioides* Finlay and Marwick, Cretaceous of New Zealand.

Procancellaria Wilckens, 1922. New Zealand Geol. Soc. Pal. Bull., no. 9, p. 21. Proposed as a genus of the Gastropoda. Type (by monotypy), *Procancellaria parkiana* Wilckens, from the Cretaceous of New Zealand. According to Finlay and Marwick (1937, p. 81), Wilckens' specimens belong to the Littorinidae.

PROGABBIA Dall, 1918. Proc. Biol. Soc. Washington, vol. 31, p. 138. Proposed as a subgenus of the genus *Cancellaria*. Type (by original designation), *Cancellaria cooperi* Gabb, Recent, west coast of North America.

PYRUCLIA Olsson, 1932. Bull. Amer. Paleontology, vol. 19, pp. 160–161. Proposed as a subgenus of *Cancellaria*. Type (by original designation), *Cancellaria solida* Sby.

RHOMBOIDESTOMA Martin, 1931. *Wetens. Meded. Mjnb. Weltevreden, vol. 18, p. 12, fig. Proposed as a subgenus of *Cancellariidae*. Type (by original designation), *Trigonostoma orcitans* Martin, sp. nov., Eocene of Java.

SCALPTIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, fasc. 18, p. 213. Proposed as a genus of the family *Cancellariidae*. Type (by subsequent designation, Cossmann, 1889, p. 15), *Cancellaria obliquata* Lam., Recent, Indo-Pacific. Jousseaume designated no type, but listed about fifteen living species under his genus. Cossmann considered *Scalptia*, as typified by *C. obliquata*, more closely related to *Trigonostoma* than to *Cancellaria* s.s.

SOLATIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, no. 19, p. 222. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Buccinum piscatorium* Gmelin, Recent, West Africa.

"Le Solat" was first used by Adanson. According to Fischer-Piette (1942, p. 218), Adanson had in hand four specimens of *Cancellaria piscatoria* (Gmelin).

SVELTELLA Cossmann, 1889. Ann. Soc. Malac. Belg., vol. 24, p. 222. Proposed as a section of the genus *Cancellaria*. Type (by original designation), *Cancellaria quantula* Deshayes, Eocene.

In 1899, Cossmann raised *Sveltella* to a genus in the subfamily *Trigonostominae*.

SVELTIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, fasc. 18, p. 214. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Cancellaria varicosa* Brocchi. Cossmann uses *Sveltia* as a genus of the subfamily *Cancellinae*, range Eocene to Pliocene.

TRIBIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, fasc. 19, p. 221. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Cancellaria angasi* Crosse (= *C. uniangulata* Deshayes, fide Dautzenberg, 1910), Recent.

TRIGONAPHERA Iredale, 1936. *Rec. Australian Mus., vol. 19, no. 5, p. 319. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Trigonostoma vinnulum* Iredale, living.

TRIGONOSTOMA Blainville, 1827. Manuel de malacologie et de conchyliologie, p. 652. Proposed as a genus. Type (by monotypy), *Delphinula trigonostoma* Lamarck, Recent, Indo-Pacific.

UXIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, fasc. 19, p. 221. Proposed as a genus of the family *Cancellariidae*. Type (by subsequent designation, Cossmann, 1889, p. 37), *Cancellaria costulata* Lam., Eocene of Paris Basin. Cossmann includes *Uxia* as a genus in the subfamily *Admetinae*, range Senonian to Miocene.

VENTRILIA Jousseaume, 1887. Le Naturaliste, ser. 2, vol. 1, fasc. 14, p. 163. Type (by monotypy), *Ventrilia ventrilia* sp. nov., Recent (?). Cossmann uses *Ventrilia* as a section of *Trigonostoma*, of value equal to *Ovilia*.

WAIPAOA Marwick, 1931. New Zealand Geol. Surv. Pal. Bull. no. 13, p. 122. Proposed as a genus of the family *Cancellariidae*. Type (by original designation), *Admete cristata* Marwick, Miocene of New Zealand.

ZEADMETE Finlay, 1926. Trans. New Zealand Inst., vol. 57, p. 429. Proposed as a genus. Type (by original designation), *Cancellaria trailli* Hutton. According to Finlay (1930, p. 242), *Zeadmete* should be a section of *Oamaruia* (q.v.). Thiele (1929, p. 353) notes that *Zeadmete* is "little different" from *Admete*.

KEY TO THE PRINCIPAL SUBGENERA OF THE CANCELLARIIDAE IN TROPICAL AMERICA

1. Whorl shoulders rounded or angulated; columella straight or bent to left; diameter of body whorl less than or equal to length of aperture 2
   Whorl shoulders flat or sunken; columella bent toward outer lip; diameter of body whorl greater than length of aperture 9
2. (*1*) Spire moderate or short; earliest sculpture cancellate; aperture subovate 3
   Spire elongate; aperture narrow 7
3. (*2*) Early whorls rounded; early sculpture evenly cancellate; columellar plaits strong; outer lip internally lirate 4
   Early whorls angulated; early sculpture with strong axials; columellar plaits thin 6
4. (*3*) Diameter of body whorl less than length of aperture; adult sculpture reticulate 5
   Diameter of body whorl equal to length of aperture; adult sculpture with heavy axial folds; outer lip strongly everted ..... *Bivetiella*
5. (*4*) Shell turreted, umbilicate; parietal wall feebly calloused; outer lip slightly everted .. *Cancellaria*
   Shell cylindrically oblong, solid, imperforate; parietal wall heavily calloused ..... *Aphera*
6. (*3*) Sculpture feeble or evanescent on body whorl; outer lip internally lirate ..... *Pyruclia*
   Body whorl with swollen axial ribs and a tendency to form spines on shoulder; outer lip internally smooth or feebly lirate ..... *Euclia*
7. (*2*) Aperture widest above center 8
   Aperture narrowly elongate; early sculpture of strong axial ribs with spiral band near posterior suture ..... *Hertleinia*
8. (*7*) First spire whorl bicarinate; adult sculpture with swollen axial ribs ..... *Narona*
   Early sculpture cancellate or reticulate; adult sculpture finely reticulate ..... *Charcolleria*
9. (*1*) Whorls with rounded shoulder; aperture ovate ..... *Bivetopsia*
   Whorls with sharply angulated or sunken shoulder; aperture trigonal ..... *Trigonostoma*

TROPICAL AMERICAN MIOCENE SPECIES OF THE CANCELLARIIDAE

The following list is arranged alphabetically by species. Subgeneric allocations are made where possible. Abbreviated references may be checked in the bibliography, which follows the list.

Cancellaria acuticarinata Weisbord, 1929. Miocene of Columbia.

C. (*Hertleinia*) *angosturana* Marks, 1949. Lower Miocene of northern Ecuador.

C. auriculaperta Vokes, 1938. A synonym of *C. cibarcola* Anderson (fide Rutsch, 1942).

C. (*Cancellaria*) *barretti* Guppy, 1866; Woodring, 1928. Miocene of Jamaica.

C. (*Cancellaria*) *bradleyi* Nelson, 1870; Olsson, 1932. Upper Miocene of Peru.

C. bulbrooki Mansfield, 1925. "Middle or lower Miocene of Trinidad."

C. casicalva Marks, 1949. Middle Miocene of southwestern Ecuador.

C. (*Bivetopsia*) *charapota* Olsson, 1942. Middle Miocene of southwestern Ecuador.

C. cibarcola Anderson, 1929; Vokes, 1938 (as *C. auriculaperta*); Rutsch, 1942. Miocene of Colombia (Tuberá formation); Upper Miocene of Trinidad.

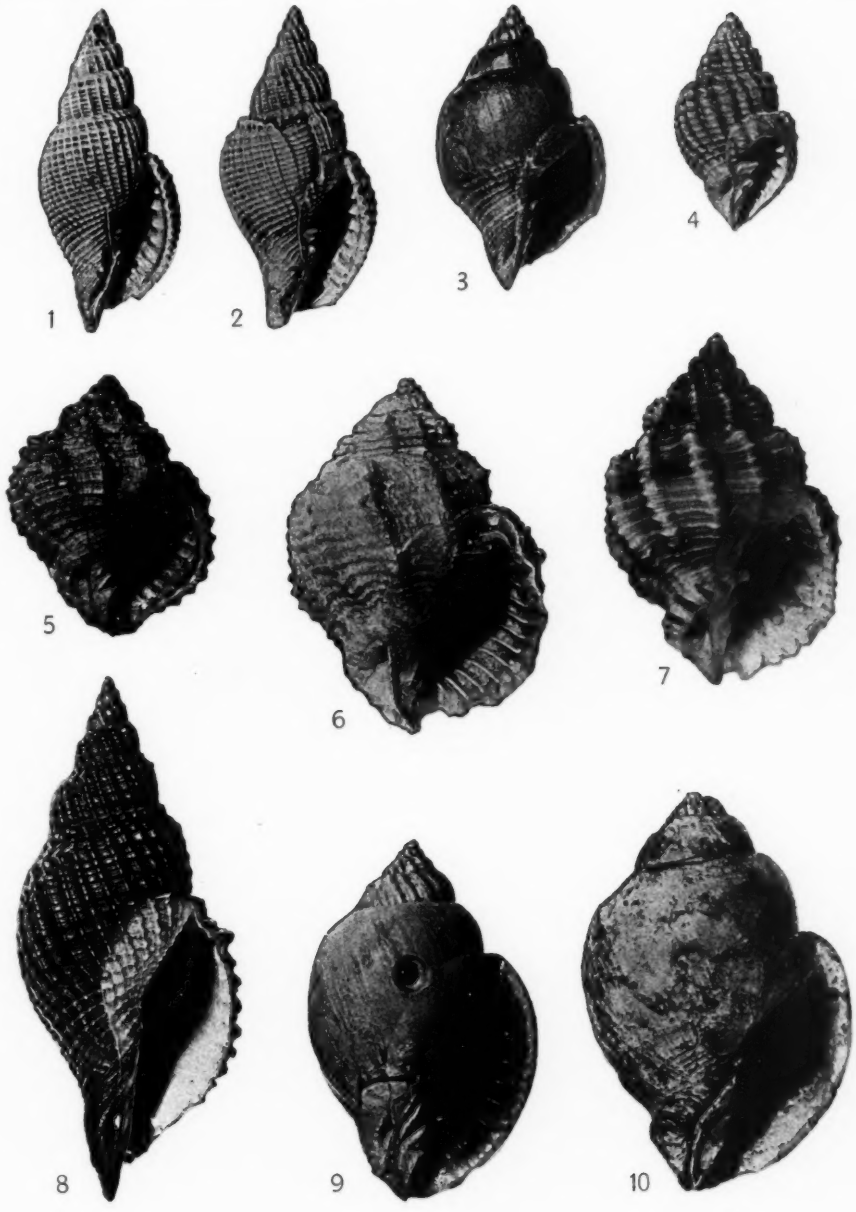
C. codazzii Anderson, 1929. Miocene of Colombia (Tuberá formation).

C. (*Cancellaria*) *cossmanni* Olsson, 1922; Anderson, 1929; Oinomikado, 1939. Miocene of Costa Rica and Colombia.

C. couvana Vokes, 1938. A synonym of *C. montserratensis* Maury (fide Rutsch, 1942).
C. (*Cancellaria*) *dariena* Toula, 1909; Brown and Pilsbry, 1911; Cossmann, 1913; Pilsbry and Brown, 1917; Olsson, 1922; Anderson, 1929; Weisbord, 1929; Oinomikado, 1939. Miocene of Panama, Costa Rica, and Colombia.
C. (*Narona*) *decaptyx* Brown and Pilsbry, 1911. Middle Miocene of Panama.
C. ellipsis Pilsbry, 1921. Miocene of Santo Domingo.
C. (*Bivetiella*) (fide Woodring, 1928) *epistomifera* Guppy, 1876; Cossmann, 1913; Maury, 1917; Pilsbry, 1921; Olsson, 1922. Miocene of Santo Domingo and Panama.
C. (*Tribia?*) *epomis* (Woodring), 1928. Miocene of Jamaica.
C. (*Bivetiella*) *frizzelli* Marks, 1949. Middle Miocene of southwestern Ecuador.
C. gabbiana Pilsbry and Johnson, 1917; Pilsbry, 1921. Miocene of Santo Domingo.
C. guppyi Gabb, 1873; Maury, 1917; Pilsbry, 1921; Anderson, 1929. Miocene of Santo Domingo and Colombia (Tuberá horizon P).
C. harrisi Maury, 1917. "Lower Miocene" of Santo Domingo.
C. hettneri Anderson, 1929. Miocene of Colombia (Tuberá horizon P).
C. (*Aphera*) *islacolonis* Maury, 1917; Gabb, 1873 (as *tessellata*); Olsson, 1922. Lower ? Miocene of Santo Domingo and Costa Rica.
C. karsteni Anderson, 1929. Miocene of Colombia (Tuberá horizon P).
C. (*Cancellaria*) *lavescens* Guppy, 1866; Woodring, 1928. Miocene of Jamaica.
C. (*Euclia*) *larkinii* Nelson, 1870; Olsson, 1932. Upper Miocene of Peru.
C. lavelana, Hodson. "Upper Middle Miocene" of Falcón, Venezuela.
C. (*Tribia?*) *losquemadica* Maury, 1917. "Middle Miocene" of Santo Domingo.
C. mauryae Olsson, 1922. Miocene of Santo Domingo and Costa Rica.
C. (*Uxia*) *miocaenica* (Cossmann), 1913. Miocene of Panama.
C. montserratensis Maury, 1925; Mansfield, 1925 (as *springvaleënsis*); Vokes, 1938 (as *ccuvana*); Rutsch, 1942. Upper Miocene of Trinidad.
C. (*Bivetopsia?*) *moorei* Guppy, 1866; Woodring, 1928. Miocene of Jamaica.
C. paraguanensis, H. K. Hodson, 1931. "Lower Miocene" of Falcón, Venezuela.
C. (*Charcolleria*) *perdiciana* Olsson, 1942. Miocene of Colombia.
C. (*Aphera*) *peruana* Nelson, 1870; Spieker, 1922; Olsson, 1932. Lower and upper Miocene of Peru.
C. (*Cancellaria*) *rowelli* Dall, 1896; Maury, 1917; Pilsbry, 1921; Olsson, 1922; Weisbrod, 1929. Miocene of Santo Domingo, Costa Rica, Colombia.
C. (*Bivetiella*) *santiagensis* Marks, 1949. Lower Miocene of northern Ecuador.
C. Pyruclia) *scheibei* Anderson, 1929. Miocene of Colombia.
C. schucherti Olsson, 1932. Upper Miocene of Peru.
C. (*Pyruclia*) *spatiosa* Nelson, 1870; Olsson, 1932. Upper Miocene of Peru.
C. springvaleënsis Mansfield, 1925. A synonym of *C. montserratensis* Maury (fide Rutsch, 1942).
C. (*Cancellaria*) *sutsalta* Marks, 1949. Uppermost lower Miocene, southwestern Ecuador.
C. (*Narona*) *trema* Olsson, 1932. Upper Miocene of Peru.
C. (*Euclia*) *triangularis* Nelson, 1870; Olsson, 1932. Upper Miocene of Peru.
C. urumacoensis H. K. Hodson, 1931. "Upper Middle Miocene" of Falcón, Venezuela.
C. venezuelana H. K. Hodson, 1931. "Upper Middle Miocene" of Falcón, Venezuela.
Trigonostoma gurabis Maury, 1917. Middle Miocene of Santo Domingo.
Trigonostoma insularis Pilsbry and Johnson, 1917; Pilsbry, 1921. Miocene of Santo Domingo.
Trigonostoma plummeri Olsson, 1922. Miocene of Panama.
Trigonostoma scalatella (Guppy), 1873; Woodring, 1928, Miocene of Jamaica.
Trigonostoma toroensis Olsson, 1922. Miocene of Panama.

EXPLANATION OF PLATE 78

FIGS. *1, 2*—*Cancellaria* (*Hertleinia*) *angosturana* Marks, n. sp., ×2. *1*, holotype. *2*, paratype. Angostura formation, lower Miocene, northwestern Ecuador. (p. 463)
3, 10—*Cancellaria casicalva* Marks, n. sp., ×2. *3*, holotype. *10*, paratype. Daule formation, middle Miocene, southwestern Ecuador. (p. 464)
4—*Cancellaria* (*Cancellaria*) *sursalta* Marks, n. sp., ×2. Holotype. Subibaja formation, uppermost lower Miocene, southwestern Ecuador (p. 461)
5—*Cancellaria* (*Bivetiella*) *frizzelli* Marks, n. sp., ×2.5. Holotype, Daule formation, middle Miocene, southwestern Ecuador. (p. 462)
6—*Cancellaria* (*Bivetiella*) *santiagensis* Marks, n. sp., ×2. Holotype. Angostura formation, lower Miocene, northwestern Ecuador. (p. 462)
7—*Cancellaria* (*Bivetiella*) *similis* Sowerby, ×2. (SU 7967). Recent, west coast of Africa. Type of *Bivetiella* Marks, subg. nov. (p. 462)
8—*Cancellaria* (*Hertleinia*) *mitriformis* Sowerby, ×2 (SU 7963). Recent, west coast of Panama. Type of *Hertleinia* Marks, subg. nov. (p. 463)
9—*Cancellaria* sp., ×2. Angostura formation, lower Miocene, northwestern Ecuador. (p. 464)



Marks, Cancellariidae

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DESCRIPTION OF SPECIES

Class GASTROPODA
Subclass STREPTONEURA
Superorder CTENOBRANCHIATA
Order PLATYPODA
Suborder TOXOGLOSSA
Family CANCELLARIIDAE
Genus CANCELLARIA Lamarck

LAMARCK, 1799, Mém. Soc. Hist. Nat. Paris, p. 71. Type (by monotypy) *Voluta reticulata* Linné, Recent, Florida and West Indies.

Subgenus CANCELLARIA s. s.

The principal distinguishing features of the subgenus *Cancellaria* are: earliest spire-whorls rather flat-sided, with regular cancellate sculpture of raised, slightly inclined axial ribs and several low spiral threads; adult sculpture reticulate or nearly so; later whorls convex; sutures barely impressed; columella with three heavy, oblique plaits; umbilicus barely open; outer lip internally lirate, with a very slight sinus or "stromboid notch"; anterior extremity with a very short canal and a moderately deep notch; no posterior notch.

Cancellaria s. s. is a prevalent stock in the tropical American Miocene strata. At least six species have been described, and many more unrecorded species are known to occur. There are, for example, at least four species, represented as yet by specimens too badly preserved to be described, in the Ecuadorean middle and lower Miocene.

CANCELLARIA (CANCELLARIA) SURSALTA Marks, n. sp.

Plate 78, figure 4

Description (based on holotype and three paratypes).—Shell small, solid, with moderately high spire, narrow aperture and regular cancellate sculpture. Protoconch of three rapidly expanding, oblique, bare whorls. First spire whorl sculptured with twelve raised axial ribs and five low spiral bands. Adult whorls with about 18 raised, evenly spaced axial ribs crossed by four or five raised spiral bands, of which the posterior band is double and forms nodes at intersections, and the next band is somewhat heavier than the two or three anterior bands. Body whorl with the double spiral band at the posterior suture, the prominent second band, and nine broad, low bands anteriorly. Sutures deeply impressed. Outer lip continuous with parietal callus. Columella with three plaits, the posterior two much the heavier. Anterior notch shallow. Outer lip internally lirate, not reinforced externally. Umbilicus slight. Dimensions of holotype: length 14.8 mm., diameter 8.4 mm.

This small, neatly sculptured species is related to *C.* (*Cancellaria*) *dariena* of the Gatun formation (Panama). It differs from *C. dariena* principally by having a more turreted spire and regular axial sculpture, with no tendency to form varices. It is assigned to the subgenus *Cancellaria* chiefly because of its evenly convex, cancellate

early spire whorls, elongate shape, and apertural characters.

C. (*Cancellaria*) *sursalta* occurs near the top of the lower Miocene strata of southwestern Ecuador, at a horizon possibly represented in the lowermost beds of the Gatun formation of Panama. A species of *Cancellaria* (*Cancellaria*) found at the lower Gatun horizon is even more closely allied to *C. dariena* than is *C. sursalta*, and is probably the direct antecedent of *C. dariena*. This lower Gatun species differs from *C. dariena* mainly by being more elongate. An analogous form, questionably referred to *C. dariena*, occurs in the basal Miocene strata of northern Ecuador.

Material.—Holotype No. 20391, Paleontological Research Institution, from the Zacachún corehole, depth 140–150 feet, Zacachún sector, Guayas Province (Progreso Basin), southwestern Ecuador. Paratypes No. 20392 (two specimens), Paleontological Research Institution; and paratype No. 7966, Stanford Univ. Paleo. type coll., from the same locality.

Subgenus BIVETIELLA Marks, n. subgen.

As mentioned above, the principal distinguishing features of the subgenus *Bivetiella* are: shape stout, with a broad body whorl; earliest spire whorl evenly convex with regular cancellate sculpture; adult sculpture cancellate; later whorls slightly carinate; outer lip internally lirate, strongly everted, and with a sinus or "stromboid notch"; anterior extremity with a short canal and a moderately deep notch; posterior notch shallow but distinct.

Bivetiella is represented in the tropical American Miocene by at least one described species, *C.* (*Bivetiella*) *epistomifera* Guppy, two more are described below, and several badly preserved specimens from the Miocene strata of Ecuador probably belong in the group. A specimen of *C.* (*Bivetiella*) *similis* from the west coast of Africa is figured on plate 78, fig. 7.

CANCELLARIA (BIVETIELLA) FRIZZELLI
sp. nov.
Plate 78, figure 5

Description (based on holotype and one paratype).—Shell rather small, low-spired, with wide aperture. Protoconch of about three rapidly expanding bare whorls. Early sculpture cancellate, of rather fine axial ribs crossed by four or five roughened spiral threads. Later sculpture of about eleven swollen axial ribs per whorl, crossed by five primary spiral cords and irregular fine spiral threads. Spiral sculpture interrupted by minute axial lines, producing intricate roughened and locally beaded appearance. Aperture subovate, wide, having outer lip continuous with parietal wall. Columella with three strong plaits and two elongate tubercles. Anterior notch shallow. Outer lip strongly everted, internally lirate. Variation noted in thickness of parietal callus and number of axial ribs per whorl, which number 11 on the holotype and 12 on the paratype. Dimensions of holotype: length 14.0 mm., diameter 11.0 mm.

The new species is distinguished by its roughened secondary sculpture and low form. In common with *C. santiagensis* of the Ecuadorean lower Miocene, it approaches the subgenus *Bivetopsia* in its wide aperture and vertical columella. No close ally from the American Miocene is known.

C. frizzelli occurs in the middle Miocene Daule formation of southern Ecuador, associated with *Potamides infraliratus* Spieker, *Conus multiliratus* Böse, *Nuculana* sp. and other forms. It is named for Dr. Don L. Frizzell, formerly paleontologist for the International Petroleum Company, who did much toward establishing the foraminiferal sequence in the Ecuadorean Tertiary rocks.

Material.—Holotype no. 20384, Paleontological Research Institution, from locality I.P.C. 1437, near the village of Jerusalém, northernmost Guayas Province (Daule Basin), Ecuador. Paratype no. 7961, Stanford Univ. Paleo. type coll., from locality I.P.C. 1457, same sector.

CANCELLARIA (BIVETIELLA) SANTIAGENSIS
Marks, n. sp.
Plate 78, figure 6

Description (based on holotype and two paratypes).—Shell of moderate size, low-spired, with wide aperture. Protoconch and first whorl not known. Early sculpture cancellate, of strong axial ribs crossed by six spiral cords. Adult sculpture of about 10 axial ribs per whorl, crossed by a strong, spine-forming spiral cord above the periph-

ery, two spiral cords posterior to the spine-forming cord, and two or three spiral cords anterior to it. Body whorl with posterior spiral cords becoming obsolescent and eight or nine spiral bands anterior to the spine-forming cord. Diameter of body whorl greater than length of aperture. Aperture having outer lip continuous with parietal wall. Parietal wall with light callus revealing underlying spirals. Columella with three strong plaits, the ends of the posterior two having two short denticles. Siphonal fasciole distinct, overlying the moderately deep anterior notch. Outer lip strongly everted, internally lirate, with thin margin, dorsally thickened. Umbilicus slight. Variations noted in number of axial ribs per whorl: the number ranges from nine to twelve on the various specimens, but is constant on any one specimen. The same condition was noted in a suite of the Recent *C. cancellata* from the west coast of Africa, in which the number of ribs per whorl varied from 10 to 15 on different specimens. Dimensions of holotype: length 23.0 mm., diameter 17.5 mm. Length of largest specimen (estimated complete) 24.5 mm.

C. santiagensis is closely allied to the Recent *C. similis* and *C. cancellata*, from both of which it differs by its wider aperture. The columellas of *C. similis* and *C. cancellata* are inclined slightly to the left; whereas the columella of *C. santiagensis* is vertical or very slightly inclined to the right, thereby approaching a character of the subgenus *Bivetopsia*. *Bivetopsia*, however, has a much larger umbilicus, flat-shouldered whorls, and more numerous spirals in the early sculpture pattern. *C.* (*Bivetiella*) *epistomifera* Guppy of the Santo Domingo Miocene has a narrower aperture and finer radial sculpture.

The new species occurs in the basal Miocene Angostura formation of northern coastal Ecuador, and in the lower Miocene Subibaja formation of southwestern Ecuador.

Material.—Holotype no. 20385, Paleontological Research Institution, from locality I.P.C. 21105, Angostura Cave on the Santiago River, Esmeraldas Province, northern Ecuador. Paratype no. 20386, P.R.I.; and paratype no. 7962, Stanford Univ. Paleo. type coll., from the same locality.

Subgenus HERTLEINIA Marks, n. subgen.

As mentioned above, the principal distinguishing features of the subgenus *Hertleinia* are: shape mitriform; earliest spire-whorls high, flat-sided, with sculpture of strong axial ribs crossed near the posterior suture by a single strong spiral band; adult sculpture evenly cancellate; aperture elongate, with a short, recurved anterior canal, moderately deep anterior notch, and barely impressed posterior notch; columella with two low folds; outer lip with distinct sinus or "stromboid notch."

The subgenus *Hertleinia* includes the Recent West Coast species *C.* (*Hertleinia*) *mitriformis* Sby. (the type species) and *C.* (*Hertleinia*) *uniplicata* Sby., and the lower Miocene species described below. A specimen of *C. mitriformis* from the west coast of Panama is figured on plate 78, fig. 8.

CANCELLARIA (HERTLEINIA) ANGOSTURANA Marks, n. sp.
Plate 78, figures 1, 2

Description (based on holotype and one paratype).—Shell of moderate size, mitriform, finely sculptured. Protoconch of three rapidly increasing, bare whorls, oblique to axis of shell. First spire whorl sculptured with eleven nearly vertical axial ribs, with a single spiral band near the posterior suture beginning at the fifth or sixth rib. Adult sculpture finely cancellate, with numerous axial ribs crossed by a low, broad spiral band at the posterior suture, a raised, broad band anterior to it, and five or six low bands on the anterior three-fourths of the whorl. Secondary spiral threads present on later whorls. Axial ribs crowded and raised at rest stages, injuries and on margin of outer lip. Aperture narrow with thin callus on parietal wall, barely distinguishable posterior notch, and deep anterior notch marked by a low siphonal fasciole. Outer lip crenate, thin on margin, thickened dorsally, internally lirate, everted anteriorly. Columella with thin callus, two thin plaits terminating in thick processes, and numerous low denticles anterior to the anterior plait. Umbilicus a thin slit. Dimensions of holotype: length 21.7 mm.; diameter 9.0 mm.

C. angosturana is distinguished by its mitriform shape and fine sculpture with two

spiral bands near the posterior suture. It is closely allied to *C. mitriformis* Sowerby, Recent, west coast of tropical America, differing from that species chiefly by its smaller size and larger terminals of the columellar plaits. The new species occurs in the Angostura formation, basal Miocene of northern coastal Ecuador. No similar species of age between early Miocene and Recent is known to the writer.

Material.—Holotype no. 20387, Paleontological Research Institution, from locality I.P.C. 21105, Angostura Cave on the Rio Santiago, Esmeraldas Province, Ecuador. Paratype no. 7964, Stanford Univ. Paleo. type coll., from the same locality.

CANCELLARIA (subgenus ?) CASICALVA
Marks, n. sp.
Plate 78, figures 3, 10

Description (based on holotype and two paratypes).—Shell of moderate size, with moderately high spire and elongate aperture. Early sculpture of strong axial ribs crossed near the posterior suture by two beaded spiral bands. Axial sculpture of about 26 raised ribs per whorl; becoming obsolescent on fourth spire whorl. Spiral sculpture of two low bands adjacent to the posterior suture, beaded where crossing axial ribs, evanescent on later whorls. Sutures deeply channeled. Outer lip continuous with parietal callus. Columella with two strong anterior plaits and one thin anterior plait. Outer lip slightly sinused, internally feebly lirate. Dimensions of holotype: length 19.0 mm., diameter 11.3 mm. Dimensions of figured paratype: length 26.3 mm., diameter 17.0 mm.

The new species is distinguished by its coronate early axial ribs and deeply channeled sutures. The subgeneric allocation is not known: it is related to *Pyruclia* through its solid shell, apertural characters and bare body whorl, and to *C.* sp. from locality I.P.C. 21105 (Angostura formation, lower Miocene) through the same features. It differs from both typical *Pyruclia* and *C.* sp. in its early sculpture, and from typical *Pyruclia* in its deeply channeled sutures. No similar species from the tropical American Miocene is known to the writer.

C. casicalva occurs in the middle Miocene Daule formation of the Daule Basin, central coastal Ecuador.

Material.—Holotype no. 20388, Paleontological Research Institution, from locality I.P.C. 1464, Jerusalém sector, northernmost Guayas Province (Daule Basin), Ecuador, Paratype no. 20389 (figured) from the same locality. Paratype no. 7965, Stanford Univ. Paleo. type coll., from the same locality.

CANCELLARIA (subgenus ?) sp.
Plate 78, figure 9

Description (based on two specimens).—Shell of moderate size, solid in appearance. Early sculpture of strong, swollen axial folds, faintly impressed by about six spiral lines. Later sculpture of twenty swollen, closely spaced axial folds per whorl, crossed by low spiral bands that are most prominent on the posterior third of each whorl and become obsolescent on the penultimate and body whorls. Body whorl sculptured with two or three very faint posterior spirals, about seven low, faint anterior spiral bands, and overlapping axial wrinkles dorsal to the outer lip. Sutures deeply channeled on the larger of two specimens, merely impressed on the smaller. Outer lip continuous with parietal callus. Columella with three strong plaits and two elongate tubercles. Outer lip internally lirate. Dimensions of figured specimen: length 23.0 mm., diameter 14.6 mm.

This species is apparently related to the subgenus *Pyruclia*, having the same apertural characters, nearly bald body whorl and moderately high spire. *Pyruclia*, as typified by the Recent species *C.* (*Pyruclia*) *solida*, has an early sculpture of strongly angulated axial ribs crossed by one or two spiral threads, and filled, level sutures: thereby it differs from the present species. The subgeneric allocation of the present species, and of *C. casicalva* Marks (q.v.) should await the discovery of more illustrative material.

The present species occurs in the basal Miocene Angostura formation of northern coastal Ecuador.

Material.—Hypotype no. 20390, Paleontological Research Institution, from locality I.P.C. 21105, Angostura Cave on the Santiago River, Esmeraldas Province, Ecuador. A second, smaller specimen from the same locality.

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REVIEW OF THE LOWER CRETACEOUS FRESH-WATER MOLLUSCAN FAUNAS OF NORTH AMERICA

TENG-CHIEN YEN[1]

THE earliest record of Lower Cretaceous fresh-water molluscan species from North America was made by Meek and Hayden in 1861 from the "head of Wind River," Wyoming. The fossil-bearing formation was quite correctly considered by these early authors to be the base of the Cretaceous system. The precise location of this original site has not been recognized, though the two species of gastropods, *Neritina nebrascensis* and *Lioplacodes veternus*, have been since recorded from Lower Cretaceous deposits exposed in the Wind River basin.

Subsequently, Lower Cretaceous molluscan faunas have been reported by T. W. Stanton (1899 and 1903) from Wyoming and Montana; W. B. Clark (1911) from Maryland and Virginia; F. H. McLearn (1929) and L. S. Russell (1932) from Alberta; F. S. MacNeil (1939) from Nevada; and the present writer (1946) from Wyoming.

Junius Henderson's comprehensive summary of American non-marine mollusks included in the Lower Cretaceous the Patapsco and the Arundel formations in Maryland and Virginia; the Trinity in Arkansas and Texas, the so-called Kootenai in Montana, the Dakota in Yellowstone Park, and the Mentor beds in Kansas. The Lower Blairmore in Alberta was not mentioned, although its molluscan species were included in his systematic account. The McMurray beds were assigned by him to equivalence with the Bear River formation.

SUMMARY OF THE LOWER CRETACEOUS CONTINENTAL BEDS AND THEIR MOLLUSCAN CONTENT

The Lower Cretaceous continental beds in North America, from which molluscan remains have been reported, may be geographically arranged under three headings: the Potomac group, which includes the Patuxent, Arundel and Patapsco formations, exposed on the Atlantic coastal plain; the upper part of the so-called Kootenai formation in Montana, the Cloverly formation in South Dakota and Wyoming, the Gannett group of Idaho, and deposits near Eureka, Nevada, in the western interior United States; the Lower Blairmore and the McMurray beds in Alberta.

The Patuxent formation rests directly on the pre-Paleozoic and early Paleozoic crystalline rocks and is overlain in places unconformably by the Arundel formation and in places by the Patapsco formation. Its flora includes a large element made up of types of ferns and cycads surviving from the older Mesozoic and another of species of gymnosperms mostly belonging to genera that range from the late Triassic to the Upper Cretaceous. A single fish has been reported but no mollusks are known.

The Arundel formation occurs unconformably on top of the Patuxent formation, and rarely comes in contact with pre-Cretaceous rocks. It is overlain unconformably by the Patapsco formation, and in places by later Tertiary and Quaternary formations. In addition to the plant remains and bones of reptiles, it contains the following species of freshwater Mollusca, which were found in a bed near Arlington, Maryland:

Cyrena marylandica Clark
Bithinia? arundelensis Clark
Viviparus marylandica Clark
Viviparus arlingtonensis Clark

The Patapsco formation is underlain in places by the Arundel formation and in places by crystalline rocks. It is uncon-

[1] The author wishes to express his thanks to the Administrative Officers of the Geological Society of America for the grant-in-aid from the Penrose Fund, which enables him to carry on this research project of fundamental importance to the stratigraphy of North America and Europe in general and the Rocky Mountain States in particular. He is also grateful to Dr. John B. Reeside, Jr. for his untiring interest in this project and his encouragement and cooperation.

formably overlain in places by later Cretaceous beds and in places by Tertiary deposits. The beds have yielded an extensive flora, but a very poor fauna. The formation is reported to be quite extensive on the Atlantic coastal plain, and intensive search should yield a richer fauna of invertebrates. So far only one species, *Unio patapscoensis* Clark, has been described.

In the western interior United States, the Lower Cretaceous deposits of continental origin are best represented by the following formations:

(1) The upper part of the so-called Kootenai formation in Montana, as conceived by most authors, i.e. the part above the unconformity described by W. A. Cobban (1945). The lower part includes the main coal beds and has yielded non-marine mollusks and plants of Jurassic age (Brown, 1946). This "upper Kootenai" has yielded fossil wood, reptilian remains, and the following species of fresh-water Mollusca, listed under the original nomenclature:

Unio farri Stanton
Unio douglassi Stanton
Viviparus montanensis Stanton
Campeloma harlowtonensis Stanton
Goniobasis? silberlingi Stanton
Goniobasis? ortmanni Stanton

It is generally considered that the beds in Yellowstone Park, Wyoming, and in western Montana assigned in the older literature to the Dakota sandstone are of the same age as the upper part of the Kootenai formation. From these beds the following species of gastropods were described by Stanton (1899) from Yellowstone Park:

Amnicola? cretacea Stanton
Goniobasis? pealei Stanton
Goniobasis? increbescens Stanton

(2) The Cloverly formation lies between the Morrison formation below and the Colorado group above. The following species of Mollusca have been described from it, listed as recorded:

Protelliptio douglassi hamili (McLearn)
Sulcatapex cretaceus Yen
Unio farri Stanton
Eupera onestae (McLearn)
Mesoneritina nebrascensis (Meek and Hayden)
Protamnicola naticoides Yen
Stantonogyra silberlingi (Stanton)
Charydrobia cretacea Yen
Lioplacodes cretaceus (Stanton)
Lioplacodes convexiculus Yen
Tortacella cf. *T. haldemani* (White)
Gyraulus sp. undet.
Lymnaea sagensis Yen
Physa cf. *P. walcotti* Yen and Reeside

(3) The beds exposed in the Eureka district, Nevada, at the northern end of Gorman Hill and south of Eureka. The beds rest unconformably on Carboniferous rocks. The following molluscan fauna was reported, again listed as originally given:

Protelliptio hamili eurekensis MacNeil
Musculiopsis russelli MacNeil
Scalez powelli (Walcott)
Viviparid ? sp.
Zaptychius carbonarius Walcott
Physa prisca Walcott
Aplexa morrisoni MacNeil
Lanx nevadensis MacNeil

(4) The Gannett Group was named from the Gannett Hills in Bannock County, Idaho, and Lincoln County, Wyoming. It includes five distinct formations—Ephraim conglomerate at the base, Peterson limestone, Bechler conglomerate, Draney limestone and Tygee sandstone, which amount to a maximum thickness of 3,200 feet. It rests on the Stump sandstone of Jurassic age.

In the Peterson limestone, as exposed in various places in the neighborhood of Afton, Lincoln County, Wyoming, the following assemblage of fresh-water molluscan species has been found. Several species of this group seem to indicate its close relationship with the fauna of the Kootenai beds in Montana.

Protelliptio cf. *P. douglassi* Stanton
Campeloma cf. *C. harlowtonensis* Stanton
Viviparus sp. undet.
Amnicola cf. *A. gilloides* Yen and Reeside
Mesocochliopa sp. undet.
Tortacella sp. undet.
Gyraulus sp. undet.
Physa sp. undet.

In the Draney limestone, fossils are reported at various localities, but the fauna is not known in detail. However, according

to Stanton,[2] it contain affinities with the faunas of the Kootenai and Bear River formations.

The name Blairmore was proposed by Leach (1913) for a formation exposed in the Blairmore area of southwestern Alberta, a series of sandstones, dark and varicolored shales, as well as several non-persistent beds of conglomerate, amounting to some 1,850 feet in thickness. It is separated from the underlying Kootenay formation by a persistent and uniform deposit of conglomerate. McLearn (1944) has used the name Blairmore as a group name, including a lower and an upper division.

Both fossil plants and invertebrates have been found at various levels within the formation, and these fossiliferous beds have been generally accepted as of fresh-water or non-marine origin. The following species of Mollusca under the original names, have been reported by McLearn (1929) from the Lower Blairmore:

Unio natosini McLearn
Unio hamili McLearn
Unio douglassi Stanton
Sphaerium onestae (McLearn)
Corbula? palliseri McLearn
Campeloma? sp.
Planorbis sp.

In an examination of the material available, I have not recognized any species of Planorbidae, but a single specimen, labelled as "*Melampus?* sp." and not in the above list, appears to be a species of *Mesoneritina* or *Neritina* in its broad sense.

On the basis of flora remains, Berry (1929) considered the Lower Blairmore to represent "the later part of Aptian and all of the Albian time" (p. 33), and he regarded "the Upper Blairmore flora as unquestionably of Upper Cretaceous age . . . would be Cenomanian in age" (p. 57). Berry's correlations have been somewhat modified by Bell (1944) and McLearn (1945), but they maintain that the basal part of the Blairmore is of Aptian age, while the remaining part of the Lower Blairmore is of Albian age.

Through the courtesy of Dr. L. S. Russell, who has borrowed from the Canadian Geological Survey some collections of the Blairmore invertebrates of several localities in Alberta, I am able to examine the material for consideration of the present work. These collections were made in Lyon Creek (McLearn 1914), Red River (Evans 1928), Pekistko Creek and Swiftwater Creek (Hage 1939), Elba River below Canyon Creek (Beach 1939), and Mill Creek (Hage 1940). These collections seem to me to indicate different horizons, possibly more than one time unit. Most of the invertebrate remains appear to be of estuarine or marine habitat; some may be of fresh-water habitat however, a positive indication of this is so far not clearly shown in the bionomic assemblages.

The McMurray formation is said to be provisionally correlated "with the unquestioned Lower Cretaceous portion of the Blairmore," and if they are not quite contemporary, the McMurray is said to be, most likely older than the Lower Blairmore. The following species of Mollusca have been reported by L. S. Russell from beds exposed along the Athabaska River in the vicinity of the Clearwater, Alberta:

Unio biornatus Russell
Murraia naiadiformis Russell
Viviparus murraiensis Russell
Viviparus sp.
Lioplacodes bituminis Russell
Melania multorbis Russell
Goniobasis? multicarinata Russell
Melampus athabascensis Russell

In examining the material available, I found two or three species contained in the above list in the collections from the so-called Lower Blairmore beds. Their occurrence seems to give a good indication of the relation of the McMurray in the north with the Lower Blairmore in the south.

Though the generic assignments made in Dr. Russell's systematic account indicate a fresh-water habitat, I am not convinced that the evidence in hand completely demonstrates it. There is little positive evidence from the fossils, except that they have comparatively simple shell features. It is difficult to imagine this fauna existing under "estuarine or near-estuarine condi-

[2] Mansfield, G. R., 1927, Geography, Geology, and Mineral Resources of Part of Southeastern Idaho: U.S. Geol. Survey Prof. Paper 152, p. 101.

tions." Further study of the material may possibly shed new light on the probable conditions of origin and on the question of whether the fauna is truly of fresh-water origin, such as the others here considered.

CHARACTERISTIC SPECIES AND HABITAT CONDITIONS

The present discussion is based mainly on the known fossil records in the Rocky Mountain area. The fauna from the apparently contemporary deposits on the Atlantic coastal plain is too imperfectly known for the time being to be included for comparison. An analysis of the molluscan faunules available seems to show that a combination of a few of the following species may be considered to indicate the presence of a Lower Cretaceous bed.

Protelliptio douglassi (Stanton)
Mesoneritina nebrascensis (Meek and Hayden)
Stantonogyra silberlingi (Stanton)
Lioplacodes cretaceus (Stanton)
"Goniobasis?" ortmani Stanton
Campeloma harlowtonensis Stanton
"Viviparus" montanaensis Stanton

However, such an assemblage can be taken only as a general indication of a continental facies of the Lower Cretaceous. This group of significant species will undoubtedly increase as the fauna becomes better known, and the additional elements may also prove to be useful in differentiating smaller age units and in determining with more assurance the conditions of origin of the fossiliferous deposits.

There seems to be little doubt that the deposits exposed near Sage Creek and Afton, Wyoming, and Eureka, Nevada, are of true fresh-water origin, for true pulmonates of aquatic habitat were found in the assemblages. The conditions of origin of the upper part of the Kootenai in Montana are less certain at present, and the Lower Blairmore and the McMurray beds in Alberta are possibly of estuarine or even marine origin. This sequence from south to north suggests that the sea was invading from the north at that time, and that an extensive delta was located somewhere in the north beyond Montana, over which the water was subject to freshening by floods discharged from the inland area, though at various intervals the delta might be actually covered by sea. Only systematic collecting and study of key exposures can test such a hypothesis, and it is premature to venture further.

CORRELATIONS

In the Potomac group, on the basis of the flora, Berry (1911, 1929) correlated the Patuxent formation with the lower part of Neocomian and he suggested correlation also with the Morrison formation in America. He also correlated the Arundel with the Kootenay in Alberta and the upper part of the Kootenai in Montana (apparently the lower part of this unit, where the plant remains are found). The most general present-day opinion is that the Morrison is definitely Jurassic, and the Patuxent Cretaceous.

The Arundel formation contains significant vertebrates, and both the Arundel and the Patapsco contain plants interpreted as later Lower Cretaceous. These formations may possibly be contemporary with the Cloverly, upper part of the so-called Kootenai in Montana, beds in the Eureka district, Nevada. The vertebrate fauna from the Arundel beds was considered by Lull (1911) to show a striking similarity to that of the Wealden of Europe. Gilmore in 1921 restudied the Arundel vertebrate fauna and concluded that the Arundel beds contain "Sauropodous dinosaurs which have been generally considered as not having survived after the close of the Morrison, and on the other hand one family of known Upper Cretaceous occurrence, and at least three other forms which have their closest resemblances with Upper Cretaceous dinosaurs." Gilmore's later work (1947) has shown that the sauropod dinosaurs actually lived into very late Cretaceous time and that they are not as a group a close indication of age. The evidence then seems to show a later Lower Cretaceous age for the Arundel and Patapsco formations. The few poorly preserved species of fresh-water mollusks from the Arundel and Patapsco formations have little value for correlation.

It has been generally recognized that the Lower Blairmore beds in Alberta are equivalent to the upper part of the so-called

Kootenai beds in Montana, although it is possible that the Lower Blairmore may represent an estuarine facies of later Lower Cretaceous in North America. On the basis of the flora, Berry concluded (1929) that these beds are close in age to the Arundel and the Patapsco formations on the Atlantic coastal plain.

The upper part of the so-called Kootenai formation in Montana, the Cloverly in Wyoming and the deposits in the Eureka District, Nevada, are probably contemporary. They seem, however, to represent different facies. Judged by the abundant occurrence of *Unio* and operculate gastropods in the upper part of the Kootenai in Montana, and in the Cloverly, these units seem to be of fluviatile origin. The deposit in the Eureka district, on the other hand, contains more pulmonates, particularly the *Ancylus*-like group and the species of *Physa*, which favor a shallow water habitat, seldom beyond a depth of a few feet. The numerous opercula of calcareous substance suggest the presence of a *Bithynia*-like group, which again may imply a shore facies. The facies of the invertebrate fauna of the deposits in the Eureka district is similar to that of the Morrison, but this resemblance is evidently due to the similar ecological conditions at the time of deposition. The new elements added to the Eureka fauna indicate the difference in age.

THE WEALDEN BEDS IN EUROPE

In correlating the Lower Cretaceous continental beds, the Wealden formation of England should be recognized as a standard of reference, with which the beds elsewhere may be compared. The molluscan faunas in the Wealden of southern England, northwestern Germany, France, and Spain seem to be quite characteristic. However, it may be noted that the so-called Wealden strata of Germany should be restricted. It is possible that only the middle part of this continental series represents the true Wealden. The lower part is an equivalent of the uppermost part of the Jurassic Purbeck; the upper part may possibly represent an estuarine facies, and it is overlain by the Hils-clays and sandstones, of Upper Neocomian age.

Despite lithologic similarity to the Purbeck beds, which lie immediately below the Wealden beds, the molluscan species of the Wealden are decidedly different from those of the Purbeck. The Wealden beds are conformably overlain in England by the Lower Greensand, and in the Lower Greensand are found some of the characteristic fossils of the Upper Neocomian beds exposed near Neuchatel in Switzerland. The Wealden beds, therefore, definitely represent a continental facies of the Lower Neocomian and the Lower Cretaceous age is conclusive.

The English Wealden beds are characterized by the presence of the following species of Mollusca:

Unio valdensis Mantell
Anodonta becklesi Newton
"Cyrena" media J. Sowerby
Viviparus sussexiensis (J. Sowerby)
Campeloma carbonaria (Roemer)
Lioplacodes elongatus (J. Sowerby)
Amnicola roemeri (Dunker)
"Paludina" scalariformis Dunker
Paraglauconia strombiformis (Schlotheim)

On the basis of the molluscan records now available, only a suggestion may be advanced as to the possible correlation of the Wealden with the North American Lower Cretaceous deposits. A more detailed study of the molluscan fauna of both North American and European Lower Cretaceous continental beds is now in progress, and more reliable conclusions may eventually be drawn.

Despite the fact that several congeneric species from the Lower Cretaceous beds of both continents show close relationship and the general assemblage (the North American Lower Cretaceous fauna is exemplified here by that of the upper part of the Kootenai in Montana) reveals similar habitat conditions at the time of deposition, my present opinion is that these North American Lower Cretaceous beds are not strictly contemporary with the Wealden. The presence of such genera as *Anodonta* and *Paraglauconia* in the Wealden suggests that the formation may represent a stage within the lower part of the Lower Cretaceous younger than that represented by the fossiliferous beds in the Rocky Mountain States. The older stage may have been re-

moved or may be very briefly represented in Europe by nonfossiliferous horizons between the Purbeck and the Wealden.

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A NEW RUDISTID FROM THE NIOBRARA OF COLORADO

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ABSTRACT—A new rudistid species, *Durania niobrarensis*, is described and figured from the Niobrara formation of the Upper Cretaceous of Colorado. Although representatives of this genus are common on the Gulf Coastal Plain, this is the first record of a *Durania* as far north as Colorado. The only other specimens of this genus in the Western Interior are recorded from the Niobrara of Kansas.

A NEW occurrence of a rudistid pelecypod has been found in the Timpas member of the Niobrara formation of northeastern Colorado. Although many representatives of this group are known from the Cretaceous of the Gulf Coastal Plain, only two have been described from the Western Interior.

The recorded distribution of rudistids in the Western Interior includes several specimens originally referred to *Radiolites maximus* Logan (1898) from the Niobrara of Kansas, and Upper Pierre specimens from Montana described as *Caprinella coraloidea* Hall and Meek (1856). Stephenson (1938) reidentified the Niobrara material as belonging to the genus *Durania* and the Pierre specimens he assigned to *Titanosarcolites* (?).

The rudistids described in the present paper were collected from the ridge of Timpas limestone at the mouth of Fourmile Canyon, sec. 12, T. 1 N., R. 71 W., about three miles north of Boulder, Colorado. The material includes imperfect and fragmentary specimens representing parts of nine individuals.

DURANIA NIOBRARENSIS Griffitts, n. sp.
Plate 79, figures 1–3

The holotype, a left valve, is incomplete at both ends, and the outer surface is only partially preserved. The shell is large, straight, broadly ovate in cross-section, and tapering gently towards the apex. The outer surface where preserved, is ribbed (pl. 79, fig. 1), the ribs being of moderate strength and numbering six to the centimeter. The main shell wall averages 25 to 30 mm. in thickness. It is composed of polygonal (4 to 8 sided) cells, averaging one millimeter in diameter. The inner shell layer as preserved is .7 mm. thick and is finely striated longitudinally and concentrically. The siphonal bands are excavated channels 30 mm. wide and 5 mm. deep (pl. 79, fig. 3). The two bands are separated by a raised interband 35 mm. wide. There is no evidence of a ligamental ridge. The right valve is unknown.

The species is colonial, the holotype being surrounded by parts of four other individuals (pl. 79, fig. 2). This holotype has the following dimensions: greatest preserved length (incomplete), 180 mm.; diameters at larger end, 145 and 120 mm.; diameters at smaller end 85 and 65 mm.; diameters of the internal cavity at large end, 80 and 55 mm.

The species is much smaller and does not generally resemble in form either of the rudistids previously described from the Western Interior. It has certain similarities in form to *Durania terlinguae* Adkins (1930), but its much greater size, finer external costae, and deeper siphonal bands distinguish it from this species. It is most closely related in form to *Durania austinensis* (Roemer). However, some confusion exists in the literature concerning the identifying characteristics of this species and its generic affinities. Böse (1906) following Roemer (1852), refers the species to the genus *Radiolites*, and in his description repeatedly emphasizes that the chief distinguishing character is the presence of a ligamental ridge. Douvillé (1908) established the genus *Durania* to include a group of rudistids which characteristically lack a ligamentary ridge. Adkins (1924) and others then assigned the species *Radiolites austinensis* Roemer to the genus *Durania* Douvillé.

In none of the Colorado specimens is a

ligamentary ridge visible. Although these specimens are fragmentary, the interior is well exposed in several individuals. Therefore, the species is assigned to the genus *Durania* Douvillé. Because the species *D. austinensis* (Roemer) apparently includes a variety of forms under the present usage, it seems more advisable to assign the Colorado forms to a new species *Durania niobrarensis*.

Types.—Holotype, Univ. Colorado Mus. 19906; paratype, Univ. Colorado Mus. 19907.

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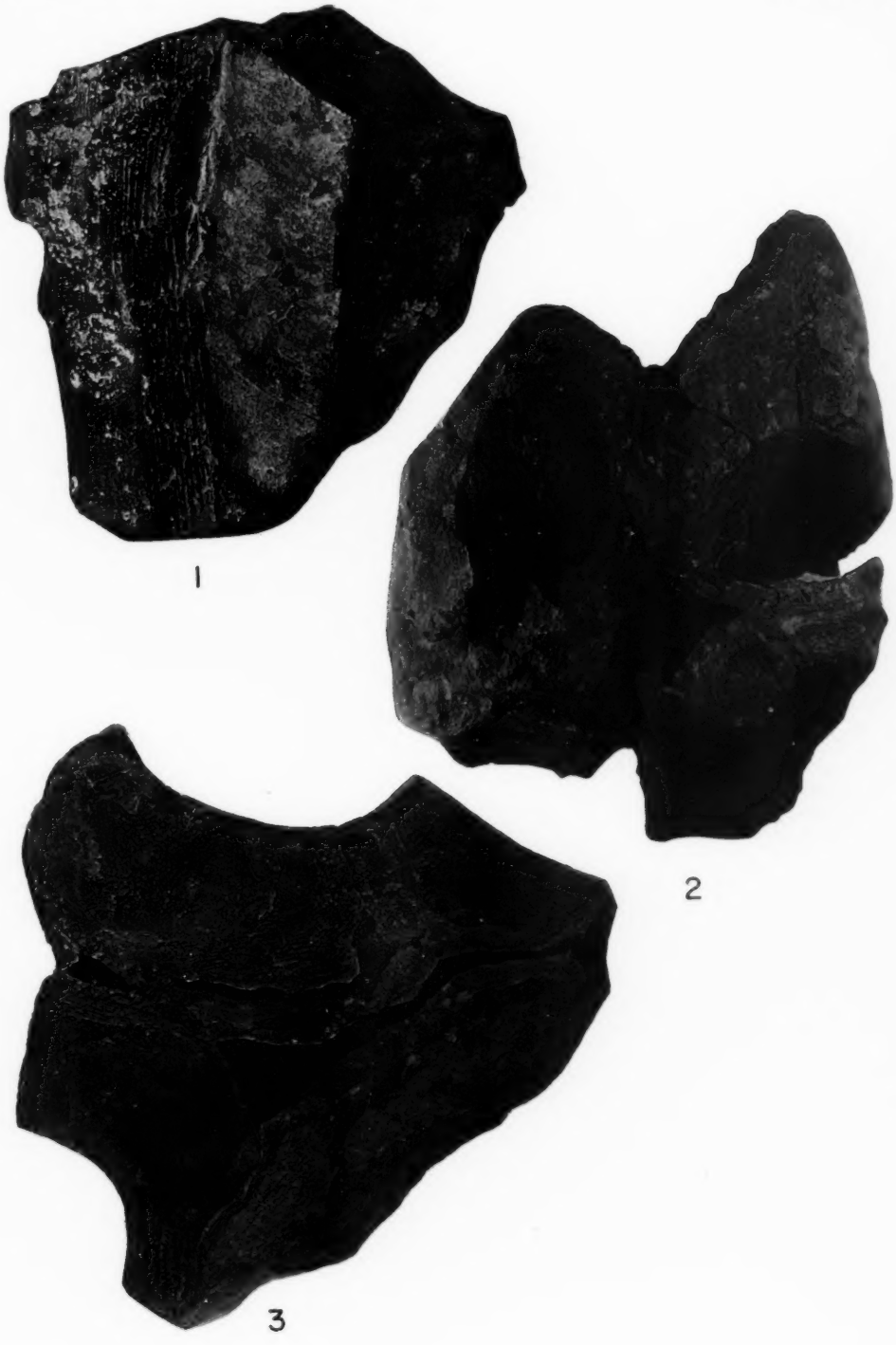
MANUSCRIPT RECEIVED FEBRUARY 4, 1949.

EXPLANATION OF PLATE 79

FIGS. *1–3*—*Durania niobrarensis* Griffitts, n. sp. *1*, the paratype (Univ. Colo. Mus. 19907), side view showing outer surface in part, ×½. *2*, the holotype (Univ. Colo. Mus. 19906), upper surface, ×⅓. *3*, paratype (Univ. Colo. Mus. 19907), upper surface showing cross section of siphonal bands, ×½.



Griffitts, Cretaceous rudistid

JOURNAL OF PALEONTOLOGY, VOL. 23, NO. 5, PP. 473–478, 2 TEXT FIGS., SEPTEMBER, 1949

FORAMINIFERA FROM THE ASAGAI FORMATION (TERTIARY) OF FUKUSHIMA PREFECTURE, JAPAN

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ABSTRACT—The Foraminifera described are from the Asagai formation near Yumoto-machi, Ishiki-gun, Fukushima Prefecture. The assemblage is correlated with that of the Vaqueros formation in California. The Asagai formation is therefore considered to be of Oligocene age on the basis of current opinion concerning the age of the Vaqueros formation. The Asagai formation also contains many Mollusca and is a good key bed for the underlying coal-bearing formations.

ACKNOWLEDGMENTS

ACKNOWLEDGMENTS are due to the following: Lt. Col. Hubert G. Schenck, Chief of the Natural Resources Section, General Headquarters, Supreme Commander for the Allied Powers, and professor of geology, Stanford University, California, under whose supervision and encouragement the present work was undertaken; Mr. L. W. Stach, Petroleum Branch, Natural Resources Section, for editing the manuscript; Professor S. Hanzawa and Dr. K. Hatai of the Institute of Geology and Paleontology, Tohoku University, Sendai, where the work was done, for advice and discussions during preparation of the manuscript.

INTRODUCTION

This paper forms part of a project initiated by Natural Resources Section, General Headquarters, Supreme Commander for the Allied Powers, for the purpose of assembling paleontologic data applicable to solution of stratigraphic problems connected with the search for oil and coal in Japan.

The fossil Foraminifera described herein were collected by the writer in 1947 from an exposure of the Asagai formation about 500 meters north of Yumoto railway station on the main Tohoku line, Yumoto-machi, Ishiki-gun, Fukushima Prefecture (37°00′30″ N. lat., 140°51′19″ E. long.). All of the specimens are now in the collection of the Institute of Geology and Paleontology, Tohoku University, Sendai.

STRATIGRAPHIC NOTES

The Asagai formation, which consists chiefly of fine sandstones grading upward into an alternation of fine sandstones and shales, is characterized by having many molluscan fossils distributed throughout, and is a good key bed for the underlying coal-bearing formations; the Foraminifera appear to be restricted to the fine sandstones.

According to Watanabe (1929), who made detailed stratigraphic studies in the Jo-Ban coalfield, the stratigraphic position of the Asagai formation is as follows, in dessending order:

Yunagaya group: Goyasu formation. Miocene.
----------unconformity----------

Shiramizu group	Shirasaka shale. 100–150 meters
	Asagai sandstone. 30–100 meters
	Iwaki sandstone. 200 meters
	Upper coal-bearing beds. 10 meters
	Shiramizu sandstone. 30 meters
	Lower coal-bearing beds. 30 meters
	Basal conglomerate. 25 meters

----------unconformity----------
Basement complex: Granitic rocks.

The Asagai formation was regarded as Miocene by Tichanovitch, Yabe, Tokunaga, Yokoyama and Watanabe, although later Watanabe expressed the view that Aquitanian might be the correct age. More recently Makiyama (1934) stated that, "Although proof is not very positive, it might be possible to introduce an approximate conclusion that the Asagai is upper Oligocene or Aquitanian in geological age," basing his conclusion on a study of the molluscan fauna.

The Foraminifera described below are of interest in that the characteristic species are related to the fauna of the Vaqueros formation at Simi Valley, Ventura County, California. Cushman and LeRoy (1938) considered this Vaqueros formation as-

semblage to be of early Miocene age, but Kleinpell's more detailed biostratigraphic study (1938) places it in the upper Zemorrian stage which Kleinpell considers is equivalent to part of the Rupelian stage (Oligocene) of the European sequence. Schenck and Childs (1942) also regarded assemblages of the Vaqueros formation as Oligocene. Because of the similarity of this assemblage from the Asagai formation to that of the Vaqueros formation at Simi Valley, the writer concludes that the Asagai formation is also Oligocene.

The Asagai assemblage consists of the following species:

Ammobaculites yumotoensis n. sp.	rare
Trochammina asagaiensis n. sp.	common
Cyclammina sp. (cf. *incisa* Stache)	few
Lenticulina fukushimaensis n. sp.	rare
Saracenaria (?) sp.	rare
Nonion cf. *boueanum* (d'Orbigny)	rare
Elphidium asagaiense n. sp.	few
Elphidium yumotoense n. sp.	common
Faujasina (?) sp.	rare
Civicides cf. *lobatulus* (Walker and Jacob)	rare
Cibicides sp.	rare

Of the species listed above, *Trochammina asagaiensis* is most common and is close to *T. palea* Cushman and LeRoy. Although there are only two specimens of *Ammobaculites yumotoensis*, they are clearly similar to *A. strathearnensis* Cushman and LeRoy. The above mentioned two species of Cushman and LeRoy together with *Cyclammina* cf. *incisa* (Stache) are characteristic members of the assemblage in the Vagueros formation at Simi Valley, Ventura County, California. It is significant that the three characteristic species of the Vaqueros formation are represented in the Asagai formation by very closely related ones.

Of the other Asagai species, *Elphidium asagaiense* is related to *E. ezoense* Asano from the Pliocene formations of Hokkaido and Karafuto and to the Recent species *Elphidiella sibirica* (Goës), which is now living in the Arctic seas. *Elphidium yumotoense* resembles *E. bartletti* Cushman, a species widely distributed in the Arctic seas. These relations indicate that the Asagai assemblage was developed in cold water, which is in agreement with the conditions indicated by the molluscan fauna.

SYSTEMATIC DESCRIPTIONS

Family TROCHAMMINIDAE

Genus AMMOBACULITES Cushman, 1910

AMMOBACULITES YUMOTOENSIS Asano, n. sp.

Figure *1*—1a, b

Test compressed, early portion involute, consisting of six or seven chambers, later uncoiled; sutures indistinct, earlier ones radial, slightly depressed, later ones oblique, not depressed; wall coarsely arenaceous; aperture terminal. Length 1.0 mm.; breadth 0.6 mm.

Remarks.—This species differs from *Ammobaculites strathearnensis* Cushman and LeRoy, from the Vaqueros formation, in the strongly oblique sutures of the later chambers.

Genus TROCHAMMINA Parker and Jones, 1859

TROCHAMMINA ASAGAIENSIS Asano, n. sp.

Figure *1*—2a–c, 3, 4a–c

Test much compressed, nearly circular, both sides flattened, umbilical region somewhat depressed; chambers seven to nine in last coil, increasing gradually in size as added, last one often subrectangular in shape; sutures slightly depressed, very slightly curved; wall coarsely arenaceous; aperture inconspicuous at margin of last chamber. Diameter up to 1.0 mm.

Remarks.—This is the most common species in the fauna of the Asagai formation. The shape of the chambers appears to have been altered by compression. This species differs from *Trochammina palea* Cushman and LeRoy in the depressed sutures in the peripheral margin of the test.

Family LITUOLIDAE

Genus CYCLAMMINA Brady, 1876

CYCLAMMINA sp. (cf. C. INCISA Stache)

Figure *1*—5, 6

All of the specimens of this species are crushed, as is common in this genus. The figures presented by Cushman and LeRoy as *Cyclammina* cf. *incisa* (Stache) from the Vaqueros formation are very close to the present form, as can be seen from a comparison of the figures of the Asagai and Vaqueros specimens.

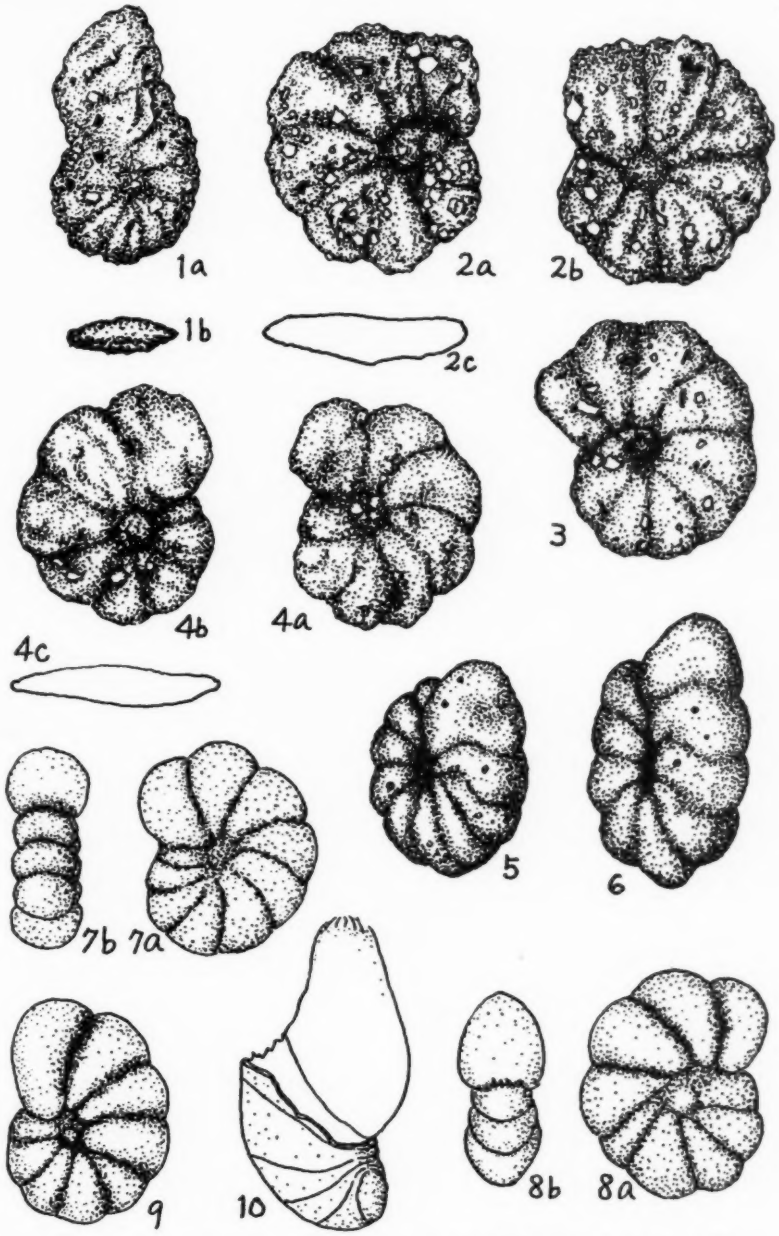

FIG. 1—Asagai formation Foraminifera, all ×40 except *5*, *6*, *10*, ×35.

1a, b, *Ammobaculites yumotoensis* Asano, n. sp. Holotype, IGPS Cat. No. 67029. a, Side view. b, Apertural view. ×40.

2a, c, *Trochammina asagaiensis* Asano, n. sp. Holotype, IGPS Cat. No. 67030. a, Dorsal view. b, Ventral view. c, Profile. ×40.

3, 4a–c, *Trochammina asagaiensis* Asano, n. sp. Paratype. ×40.

5, 6, *Cyclammina* sp. cf. *C. incisa* (Stache). Hypotype, IGPS Cat. No. 67051. ×35.

7a, b, *Elphidium yumotoense* Asano, n. sp. Holotype, IGPS Cat. No. 67035. a, Side view. b, Apertural view. ×40.

8a, b, 9, *Elphidium yumotoense* Asano, n. sp. Paratype. ×40.

10, *Saracenaria* (?) sp. ×35. Hypotype, IGPS Cat. No. 67038.

Family NODOSARIIDAE
Genus LENTICULINA Lamarck, 1804
LENTICULINA FUKUSHIMAENSIS Asano, n. sp.
Figure *2*—3a, b

Test close-coiled, biconvex, slightly umbonate; periphery angled; chambers about 14 in last coil, not inflated; sutures distinct, gently curved in later ones, but indistinct in earlier ones; surface smooth; aperture inconspicuous, without median slit at apertural face. Diameter up to 1.0 mm.

Remarks.—This species differs from *Lenticulina kamakuraensis* Asano, a common Neogene species of Japan, in the more depressed and less distinct sutures.

Genus SARACENARIA Defrance, 1824
SARACENARIA (?) sp.
Figure *1*—10

The chambers of the incomplete specimen here figured reveal the characters of the genus *Saracenaria*, but the later portion is broken and therefore its specific identity cannot be established.

Family NONIONIDAE
Genus NONION Montfort, 1808
NONION cf. BOUEANUM (d'Orbigny)
Figure *2*—4a, b

The topotype of *Nonion boueanum* (d'Orbigny) was figured by Cushman in his monograph of the Nonionidae and, compared with the present form, the Asagai specimen has a more depressed test. and a less granular umbo. In regard to d'Orbigny's species, Cushman stated that, "There are records for central and southern Europe from the upper Oligocene to the Pliocene which may represent this species, but those from the other regions evidently do not."

Genus ELPHIDIUM Montfort, 1808
ELPHIDIUM ASAGAIENSE Asano, n. sp.
Figure *2*—1a, b, 2

Test rather large, periphery broadly rounded, not lobulated, umbonate with granular shell material; chambers as many as 15 in last coil, slightly inflated in later ones; sutures gently curved, depressed, retral processes very short, often indistinct; wall smooth; aperture low openings at base of apertural face. Diameter about 1.5 mm.; breadth 0.5 mm.

Remarks.—This species differs from *Elphidium ezoense* Asano in its almost entire periphery of the test and by the less distinct retral processes. Some specimens show the characters of *Nonion* without clear retral processes.

ELPHIDIUM YUMOTOENSE Asano, n. sp.
Figure *1*—7a, b, 8a, b, 9

Test with earlier coils visible in umbilical region, which is depressed, periphery broadly rounded, lobulated; chambers distinct, inflated, nine or ten in last coil; sutures distinct, depressed, retral processes very short, often hardly visible; wall smooth, finely perforate; aperture formed by small pores along base of apertural face. Diameter up to 0.8 mm.; thickness about 0.3 mm.

Remarks.—This species is common in the present collection. The retral processes of the sutures are often invisible. In this respect, *Elphidium yumotoense* n. sp. resembles *E. bartletti* Cushman, which is widely distributed in the circum-arctic region.

Genus FAUJASINA d'Orbigny, 1839
FAUJASINA (?) sp.
Figure *2*—5a–c

Only a single specimen of this genus was found in the collection. The test is depressed, but trochoidal; the flattened side shows the earlier whorls, while the convex side is involute. The retral processes of the sutures are very short on both sides. Although the characters of the genus *Faujasina* were well displayed by the single specimen, more material is necessary before a complete description can be given.

Family ROTALIIDAE
Genus CIBICIDES Montfort, 1808
CIBICIDES cf. LOBATULUS
(Walker and Jacob)
Figure *2*—7a, b

Several incomplete specimens referable to this species were found in the collection. The preservation is by no means perfect, but the characters of the chambers agree with those of *C. lobatulus*, although the test is more depressed than the typical form.

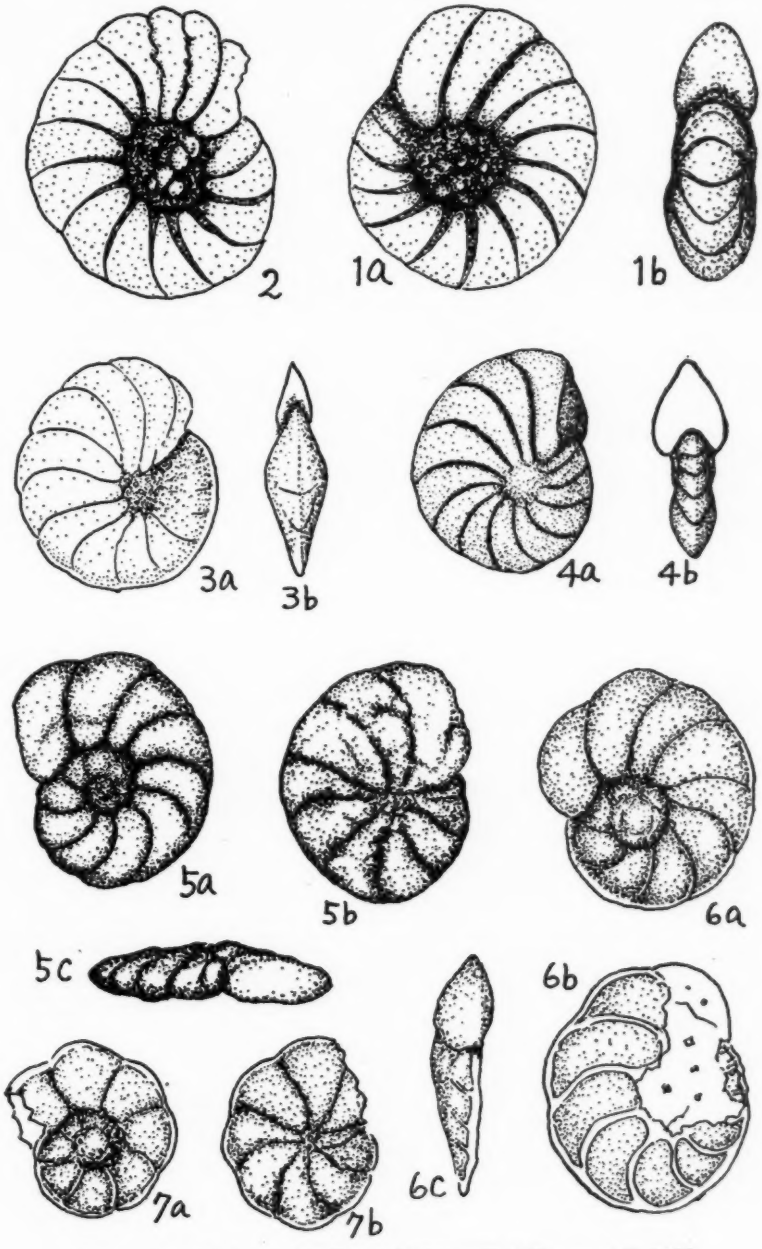

FIG. 2—Asagai formation Foraminifera, all ×40 except 7, ×35.

1a, b, *Elphidium asagaiense* Asano, n. sp. Holotype, IGPS Cat. No. 67034. a, Side view. b, Apertural view. ×40.

2, *Elphidium asagaiense* Asano, n. sp. Paratype. ×40.

3a, b, *Lenticulina fukushimaensis* Asano, n. sp. Holotype, IGPS Cat. No. 67032. a, Side view. b. Apertural view. ×40.

4a, b, *Nonion* cf. *boueanum* (d'Orbigny). Hypotype, IGPS Cat. No. 67033. a, Side view. b, Apertural view. ×40.

5a, b, c, *Faujasina* (?) sp. Hypotype, IGPS Cat. No. 67036. a, Flattened side. b, Convex side. c, Apertural side. ×40.

6a, b, c, *Cibicides* sp. Hypotype, IGPS Cat. No. 67014. a, Convex side. b, Flattened side. c, Apertural side. ×40.

7a, b, *Cibicides* cf. *lobatulus* (Walter and Jacob). Hypotype, IGPS Cat. No. 67037. a, Flattened side. b, Convex side. ×35.

CIBICIDES sp.
Figure *2*—6a–c

The incomplete specimens show only that the convex side is somewhat evolute, and the coil of the flattened side is not visible. Accordingly, more material is needed for specific determination.

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JOURNAL OF PALEONTOLOGY, VOL. 23, NO. 5, PP. 479–480, PL. 80, SEPTEMBER 1949

THE FORAMINIFERAL GENUS *CRUCILOCULINA* D'ORBIGNY, 1839

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ABSTRACT—The foraminiferal genus *Cruciloculina* d'Orbigny, 1839 has been regarded as a synonym of *Triloculina* by many authors. However, the aperture of *Cruciloculina* is cruciate in the young and labyrinthic in the adult and there is no development of a tooth. For such reasons and from observations on a complete series of specimens showing the development of the aperture in material from the Pliocene Sawane formation, Sado Island, Niigata Prefecture, Japan, the author considers *Cruciloculina* to be valid. The diagnosis of the genus *Cruciloculina* is emended herein.

ACKNOWLEDGMENTS

ACKNOWLEDGMENTS are due to the following persons: Lt. Col. Hubert G. Schenck, Chief of the Natural Resources Section, General Headquarters, Supreme Commander for the Allied Powers, and Professor of Geology, Stanford University, California, under whose supervision and encouragement the present work was undertaken; Mr. Leo W. Stach, Petroleum Branch, Natural Resources Section, General Headquarters, Supreme Commander for the Allied Powers; and Dr. K. Hatai of the Institute of Geology and Paleontology, Tohoku University, Sendai, for editing the manuscript.

INTRODUCTION

In 1839 d'Orbigny established the genus *Cruciloculina* for foraminifers with cruciate instead of milioline apertures, and with chambers of the same arrangement as *Triloculina*. Subsequently Brady treated *Cruciloculina triangularis* d'Orbigny, the genotype of *Cruciloculina*, as a synonym of *Triloculina tricarinata* d'Orbigny, 1826, on the opinion that the characters of the aperture are highly variable. Cushman (1917) found among the material from the "Albatross" station D 5056, off Japan in 258 fathoms, a form similar to d'Orbigny's type, but stated that sufficient material was not available for a study of the young stages for comparison of them to similar stages of *Triloculina tricarinata*. Although later authors have not reported the occurrence of *Cruciloculina*, the writer found many specimens of a cruciate type of Foraminifera from the Pliocene formations from the borderland of Japan, namely, from the lower part of the Sawane formation in Sado Island, the Natsukawa formation in Niigata Prefecture, and from the middle and lower parts of the Setana formation in southwest Hokkaidô.

The newly obtained material from the Pliocene formations is sufficient for studying the development of the aperture. The aperture in *Cruciloculina* is cruciate in the young and labyrinthic in the adult, while in *Triloculina* the aperture is provided with a bifid or plate-like tooth. For these reasons *Cruciloculina* can be distinguished from *Triloculina*.

The emended generic diagnosis of *Cruciloculina* is as follows:

Family MILIOLIDAE

Genus CRUCILOCULINA d'Orbigny, 1839

Genotype.—Cruciloculina triangularis d'Orbigny 1839.

Test similar to *Triloculina*, but differing from it by possessing a simple, linear or bifid aperture instead of tooth in earlier stages, becoming "X"-shaped with slight lips around the aperture in later stages and finally attaining a compound or labyrinthic aperture.

Range.—Tertiary to Recent.

d'Orbigny's original figures of *Cruciloculina* show an "X"-shaped aperture similar to pl. 80, figure 1, but he evidently did not possess material sufficient for a study of the development of the aperture.

The apertural characters of *Triloculina* are linear or with a bifid tooth (figs. 3–5), or

with a plate-like tooth in large forms. However, in *Cruciloculina* the aperture does not develop a tooth, and is linear or bifid in early stages (figs. 8, 9), and "X"-shaped with slight lips around the apertural openings (figs. 1, 2, 6) and finally attains a compound or labyrinthic one (figs. 7, 10, 11, 12, 13) in the full adult. The peculiar series of apertural development is a distinct feature in *Cruciloculina*.

CRUCILOCULINA JAPONICA Asano, n. sp.
Plate 80, figures 1, 2, 6–13

Test similar to *Triloculina trigonula* (Lamarck), but differing in possessing apertures "X"-shaped or labyrinthic in adult; peripheral angle of inflated chambers broadly rounded, sometimes carinate. Margins of test more rounded than in *C. triangularis* D'Orbigny.

Length ca. 1.5 mm.; breadth 1.0 mm.

This species is very common in the Lower part of the Sawane formation (Pliocene) at the type locality, which is near Sawane-Machi, Sado-Gun, Niigata Prefecture (Lat. 37°59′47″ N., Long. 138°16′43″ E.), Japan. Other localities for this species are: Boring core sample (Natsukawa formation) from a depth of 120 meters at Shimotaka-Machi, Arahama-Mura, Kariha-Gun, Niigata Prefecture; Cliff on the Toshibetsu river (Setana formation) about 800 meters west of Omagari, Toshibestu-Mura, Setana-Gun, Hokkaido; and, roadside cut (Setana formation) about 200 meters west of Maruyama, Toshibestu-Mura, Setana-Gun, Hokkaidô.

MANUSCRIPT RECEIVED JANUARY 5, 1949.

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EXPLANATION OF PLATE 80

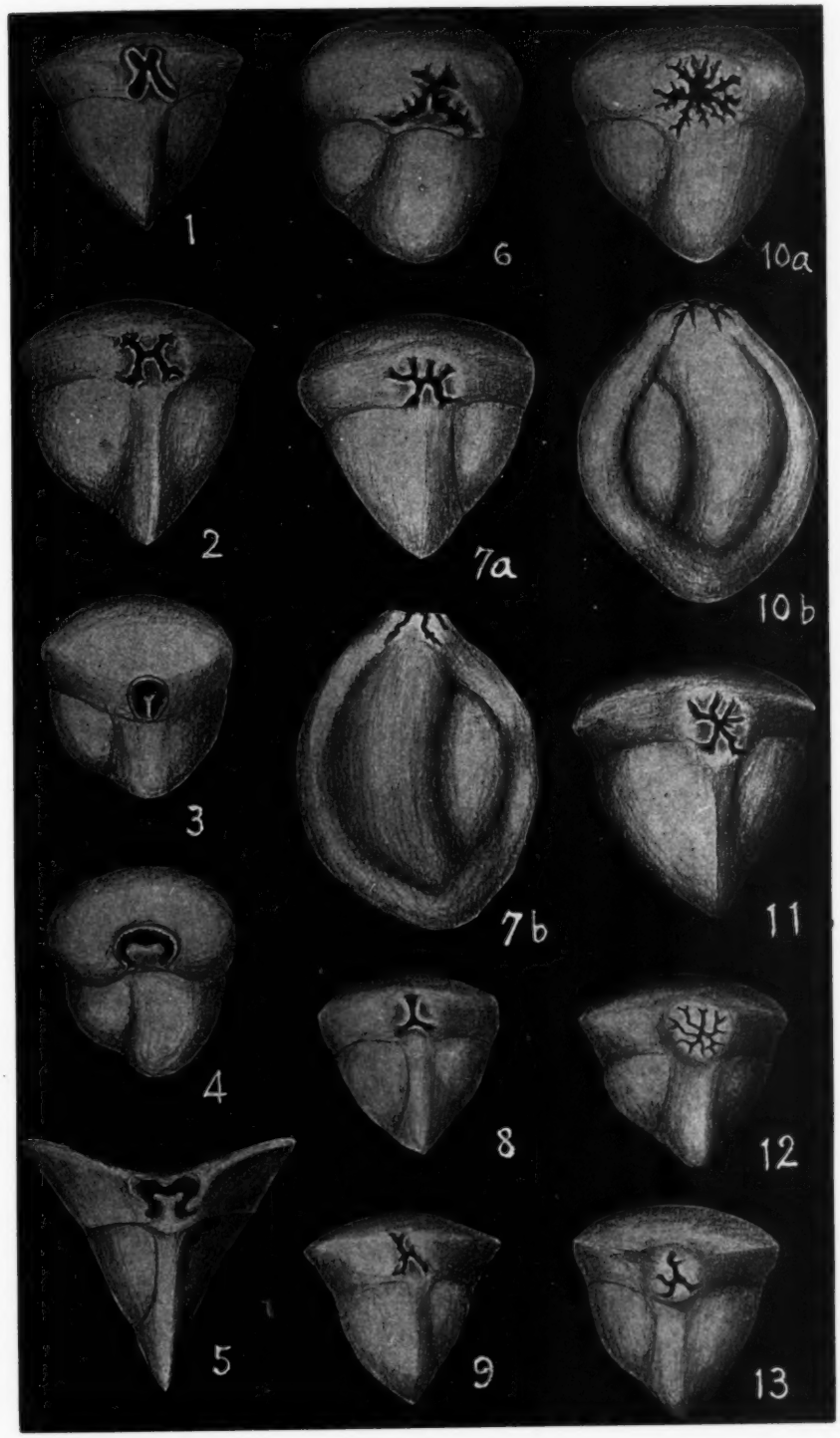
FIGS. *1, 2, 6—Cruciloculina japonica* Asano, n. sp. Note the "X" shaped aperture. Paratypes from the lower part of the Sawane formation (Pliocene), Sawane-Machi, Sado-Gun, Niigata Prefecture.

3, 4—Triloculina trigonula (Lamarck). Showing the bifid or plate-like tooth of the aperture. Hypotypes from the Hosoya formation (Pliocene), from a roadside cut between Hosoya and Tonbe, Haranotani-Mura, Ogasa-Gun, Shizuoka Prefecture.

5—Triloculina tricarinata d'Orbigny. Showing the plate-like tooth of the aperture. Hypotype from the Hosoya formation (Pliocene), from a road-side cutting between Hosoya and Tonbe, Haranotani-Mura, Ogasa-Gun, Shizuoka Prefecture.

7a, b, 10a, b, 11, 12, 13—Cruciloculina japonica Asano, n. sp. Showing the labyrinthic aperture. *10*, Holotype (IGPS, Cat. No. 67015), from the lower part of the Sawane formation (Pliocene), near Sawane-Machi, Sado-Gun, Niigata Prefecture. *7, 11, 12, 13*. Paratypes, from the Setana formation (Pliocene), from a cliff of the Toshibestu river, about 800 meters west of Omagari, Toshibetsu-Mura, Setana-Gun, Hokkaidô.

8, 9—Cruciloculina japonica Asano, n. sp. Showing the bifid aperture of a young individual. Paratypes, Setana formation (Pliocene), from a cliff of the Toshibetsu river, about 800 meters west of Omagari, Toshibetsu-Mura, Setana-Gun, Hokkaidô. All figures are magnified ×48.



Asano, *Cruciloculina*

JOURNAL OF PALEONTOLOGY, VOL. 23, NO. 5, PP. 481–495, 20 TEXT FIGS., SEPTEMBER 1949

ROTALIID FORAMINIFERA OF THE CHAPMANININAE: THEIR NATURAL DISTINCTION AND PARALLELISM TO THE *DICTYOCONUS* LINEAGE

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ABSTRACT—The new rotaliid subfamily Chapmanininae comprises three genera, characterized by a trochoid-to-uniserial plan of growth and multiple apertures leading into internal tubes. Synopsis of the subfamily: *Ferayina*, new genus (genotype *F. coralliformis*, new species; also *F. peruviana*, new species)—outer wall coarsely perforate, septum imperforate and single (middle Eocene of Texas; upper Eocene of northwestern Peru); *Chapmanina* Silvestri (genotype *Chapmania gassinensis* Silvestri)—wall and septum double, imperforate, with intra-septal spaces, one row of peripheral chamberlets present (middle? and upper Eocene of southern Europe); *Preverina*, new genus (genotype *Chapmania galea* Silvestri)—septum single, with several rows of peripheral chamberlets, apertures and tubes vestigial (Oligocene? to middle Miocene of Italy). *Chapmania* apparently was derived from *Ferayina*, but the derivation of *Preverina* is doubtful. "*Chapmania*" *sertata* Silvestri is questioned, and "*C.*" *kiliani* Prever and *silvestrii* Prever apparently belong to *Orbitolinopsis* Silvestri. The similarity of *Chapmanina* and its allies to *Dictyoconus* Blanckenhorn and related forms is due to parallel response to the requirements of structural reinforcement.

INTRODUCTION

AUTHORITIES disagree on the taxonomic position of the southern European Eocene foraminiferal genus *Chapmanina* Silvestri. Cushman (1948, p. 310) places the genus provisionally in the Cymbaloporidae, although recognizing the possibility of rotaliid affinities. Chapman and Parr (1936, p. 144) included it in the subfamily Planorbulininae within an extended family Rotaliidae. Glaessner (1945, p. 153) followed essentially the same course, but recognized a family Planorbulinidae and subfamily Planorbulininae. Galloway (1933, pp. 318, 320) made the genus (under an unavailable name) the type of a composite family Chapmaniidae. Apparently none of these workers had examined specimens of *Chapmanina*, so their perpetuation of Silvestri's errors of interpretation is not surprising, even though his published photomicrographs show clearly the morphology of the genus. The fundamental reason for lack of agreement is to be found in the absence of an intermediate form to connect the genus with some established lineage.

The requisite connecting link has been found in *Ferayina coralliformis*, new genus and species, a tiny but structurally complex foraminifer from the Weches formation (middle Eocene) of Texas. Obvious similarities to *Chapmanina* were observed in this form, but with some puzzling differences. In resolving these apparent anomalies, a restudy of *Chapmanina* was undertaken, based upon figures and descriptions. Although no specimens were available for examination, Silvestri's excellent photomicrographs, sketches, and structural diagrams, supplemented by his very detailed descriptions, are adequate to allow correction of current errors in diagnosis of the genus.

The contributions of this paper, some of which have appeared previously in abstract (Frizzell, 1947), are briefly as follows: *Chapmanina* is shown to begin as an abbreviated trochoid spiral followed by a series of uniserial chambers with peripheral chamberlets, rather than having a subsequent pattern of annular chambers. The wall of the test is double, with intra-septal spaces; the supposed "subarenaceous" third wall is simply the calcite-filled space between the septal sheets. The double wall seems to have been understood by Vaughan (1928, p. 283; in discussion of *Cushmania fontabellensis*) and probably in later years by Silvestri, but neither author followed out the taxonomic implications of this observation. The intermediate genus *Ferayina* is

simpler in having a single wall, and in lacking peripheral chamberlets. *Preverina*, new genus, has a development of septal chamberlets, but a single wall. Galloway's family Chapmaniidae is replaced by a new subfamily Chapmanininae, differing in the addition of *Ferayina* and *Preverina*, and in the elimination of *Halkyardia* Heron-Allen and Earland and *Dictyoconoides* Nuttall. The name *Chapmanina* is insecure, requiring a decision by the International Commission on Zoological Nomenclature.

The genus *Chapmanina* has been confused with *Dictyoconus* Blanckenhorn. The latter, however, is fundamentally distinct and belongs to the valvulinid subfamily Ataxophragmiinae. The similarity of structures in these genera and their related lineages is explained in this paper as an example of parallel evolutionary responses to fit the mechanical requirements of conical shape.

Acknowledgments.—I am indebted to Mrs. Helen J. Plummer for showing me the outcrop at Smithville, Texas, which furnished the types of *Ferayina coralliformis*, and for information regarding the stratigraphy of that area. Dr. Dan E. Feray, of the Bureau of Economic Geology, Austin, Texas, generously relinquished his priority to study of the Weches foraminifer. Dr. Brooks F. Ellis, of the American Museum of Natural History, has furnished references that were otherwise unavilable to me. In addition, I gratefully acknowledge the help given by Dean R. Z. Williams, of the Missouri School of Mines and Metallurgy, in a discussion of foraminiferal morphology from the viewpoint of structural engineering. Original illustrations were drawn by Mrs. Sarah B. Martin, Austin, Texas, for figures 1–4, 16–20.

SYSTEMATIC DISCUSSION

ORDER FORAMINIFERA

FAMILY ROTALIIDAE

SUBFAMILY CHAPMANININAE

Frizzell, new subfamily

Chapmaniidae GALLOWAY (*in part*), 1933, Man. Foraminifera, pp. 316–321 (nomenclaturally invalid because based upon a homonym).

Diagnosis.—Test calcareous-perforate, small, free, conical, with flat or convex base. Simple forms with test composed of a coarsely perforate wall and an imperforate septum; advanced forms with septum replacing perforate wall, septum sometimes double and with intra-septal spaces. Plan of growth a trochoid spiral, followed by a uniserial series of low chambers extending in the direction of the axis of the trochoid coil; septa of uniserial chambers invaginating into tubes (*Ferayina*), tubes and annular chamberlets (*Chapmanina*), or annular and central chamberlets with vestigial tubes (*Preverina*). Apertures provided by openings of tubes.

Range.—Middle Eocene to middle Miocene; Mediterranean region, Gulf Coast of the United States, and western South America.

Relationships.—The Chapmanininae presumably developed from the Rotaliinae. A uniserial plan of growth was added, with progressive reduction of the trochoid initial coil, accompanied by development of multiple tubular apertures and increasing specialization of the septum. *Chapmanina* is believed to have arisen from *Ferayina* by invagination of the septum into peripheral chamberlets, the septal element having replaced the perforate wall of the ancestral form. The consequent loss of perforations for communication of protoplasm was compensated by development of a double septal wall and a system of intraseptal spaces. The derivation of *Preverina* is less clear, and that genus may even have descended from another rotaliine ancestor. *Chapmanina* has been confused with *Dictyoconus* Blanckenhorn, but the resemblances are superficial rather than of genetic significance.

The subfamily is a coherent unit as redefined here. Galloway's family Chapmaniidae was both composite and erroneously diagnosed, including forms described as having "chambers . . . arranged spirally in the form of a hollow cone, the inside of the cone filled with a calcareous deposit or with secondary chambers." Restudy of the type genus shows that this definition is not applicable, inasmuch as *Chapmanina* is mainly uniserial. *Halkyardia* Heron-Allen and Earland (in Halkyard, 1918, p. 107) and *Dictyoconoides* Nuttall (1925, p. 384), the other two components of Galloway's Chapmaniidae, appear to fit the

general definition. Rather obviously, however, the two forms are not closely related. *Halkyardia* may belong to the Cymbaloporidae, as indicated by Cushman (1948) or even to the Planorbulinidae, as Chapman and Parr (1936) and Glaessner (1945) believed. *Dictyoconoides* is distinguished by a double spiral of later chambers. It is a rotaliid of uncertain subfamily position. Elimination of both genera from the Chapmanininae cannot be avoided.

Bermudez (1948) is remarkably similar to *Ferayina* in superficial appearance. It is distinguished, however, by its single, narrow, semi-circular aperture with internal tubes at the ends. Cushman and Bermudez refer their genus to the Buliminidae.

Remarks.—The genus is named in honor of Dan E. Feray, who currently is monographing the foraminiferal fauna of the Weches formation.

KEY TO GENERA

Wall single; initial spiral comprising about one-third of test—
Septum invaginating into tube-pillars; without peripheral chamberlets..... *Ferayina*, new genus
Septum invaginating into peripheral chamberlets; tube-pillars vestigial..... *Preverina*, new genus
Wall double; initial spiral greatly reduced; septum invaginating into a peripheral row of annular chamberlets and central tube pillars..... *Chapmanina* Silvestri

Genus FERAYINA Frizzell, new genus

Genotype.—*Ferayina coralliformis* Frizzell, new species.

Diagnosis.—Test free, very small (about 0.3 mm. diameter in genotype to 0.6 mm. diameter in *F. peruviana*), conical, with flat base, consisting of an initial trochoid spiral followed by a uniserial series of chambers extending in the direction of the axis of the initial coil; wall calcareous, differentiated into an imperforate septum and a coarsely perforate outer wall, external secondary deposits thickening and covering these elements without appreciably changing their nature; apertures numerous, circular, formed by invagination of the septum into cylindrical tube-pillars that end abruptly at the preceding septum; communication of protoplasm takes place through large pores at base of tubes and through mural perforations.

Range.—Middle Eocene (Claiborne group, Weches formation) of Texas; lower part of upper Eocene (Talara shale, middle faunal division) of northwestern Peru.

Comparisons.—*Ferayina* is closely related to *Chapmanina* Silvestri and *Preverina*, new genus. It is distinguished from *Chapmanina* by the single wall and relatively larger initial coil, as well as by the absence of a marginal trough and peripheral chamberlets. *Ferayina* differs from *Preverina* in the lack of septal chamberlets and in the greater development of tube-pillars. *Colomia* Cushman and

FERAYINA CORALLIFORMIS Frizzell, new species
Figures 1–3, 4a–b, 19

Description.—Test free, very small (0.36 mm. maximum height observed), conical, usually slightly compressed, strongly resembling a minute solitary coral. Apex of test slightly asymmetrical, acute in microspheric and broadly rounded in megalospheric form; base approximately flat; diameter/height ratios from 80% to 132%, typically 80–90%. Test sculptured with numerous fine, low longitudinal ribs, with very narrow interspaces, which increase in number with growth by intercalation; ribs 20–34 in number, typically 28–32, absent from last one or two chambers where secondary deposits have not accumulated. Apertures numerous and variable in number, decreasing in number with age, circular, closely spaced, comprising concentric rows, formed by invagination of the septum into cylindrical tube-pillars. An immature paratype shows 39 apertures grouped in 3 rows around a central identical aperture; a more mature paratype has 2 rows with 13 peripheral and 5 central apertures; and another mature paratype has 2 rows with 10 and 4 apertures, respectively. Dimensions of a suite of paratypes are shown in Table I.

In vertical section the test is seen to begin with a trochoid spiral of about three whorls. The extremely small size of the initial chambers makes their description impossible at

present, although the trochoid pattern is indisputable. Following the initial spiral is an expanding linear series of uniserial chambers, of which a maximum of 10 have been counted in the suite of sections examined. Their axis is essentially parallel to the axis of the initial coil. The septum is imperforate and extends to the periphery of the test, whereas the outer wall is coarsely perforate. The sides of the test are covered by secondary deposits which cover the septum and outer wall and are thickest in the earlier part of the test. The secondary deposits are penetrated by continuations of the mural pores. The tubes of the septa connect with preceding septa and end abruptly, not lining up to form connections through succeeding septa. Communication of protoplasm in the last chamber apparently was through single large pores at the base of each tube. Earlier chambers, however, seem to have communicated mainly if not entirely through the mural perforations.

TABLE I. Dimensions of a suite of paratypes of *Ferayina coralliformis*.

Specimen number	Height (mm.)	Diameter (mm.)	Maximum number of ribs (approx.)
1	0.25	0.33	22
2	0.29	0.25	24
3	0.29	0.25	28
4	0.29	0.31	20
5	0.31	0.31	28
6	0.33	0.30	30
7	0.33	0.31	32
8	0.33	0.33	30
9	0.36	0.29	32
10	0.36	0.30	34

Type locality.—Smithville, Bastrop County, Texas; south bank of the Colorado River, approximately 0.1 mile west of the highway bridge; about the middle of Stenzel's Bed II-c (H. B. Stenzel, manuscript), a highly glauconitic greenish-gray shale immediately below an indurated stratum with abundant pelecypods, near the base of the exposure. Collected by Helen J. Plummer, D. L. Frizzell, and H. E. Frizzell, March 3, 1946.

Occurrence.—Weches formation, Claiborne group, middle Eocene of Texas. A detailed list of occurrences will be given in a forthcoming paper by Dan E. Feray.

Disposition of types.—The holotype and published paratypes have been deposited in the Cushman Laboratory for Foraminiferal Research, Sharon, Massachusetts.

Comparisons.—*Ferayina coralliformis* is similar to *F. peruviana*, but is considerably smaller and typically has a smaller angle of the test. Its longitudinal ribs are coarser, more closely spaced, and fewer, and increase in number by intercalation rather than by branching. In addition, *F. coralliformis* has fewer apertures than in the holotype of *F. peruviana*.

Remarks.—The species is rare. More than 185 specimens have been assembled, however, by means of carbon tetrachloride flotation of the finer fractions of washed residues. Three specimens have been found that show an interesting abnormality that is not common among Foraminifera, although it has been noted in unpublished studies of *Orbitolina texana* (Roemer) (figure 2). Two young individuals joined their protoplasm, apparently both at the point of initiating the uniserial portion of their tests. They fused test and protoplasm, continuing to form a single cone that is normal except for its bifurcate apex. This variant was able to reach maturity in *Ferayina*, although the

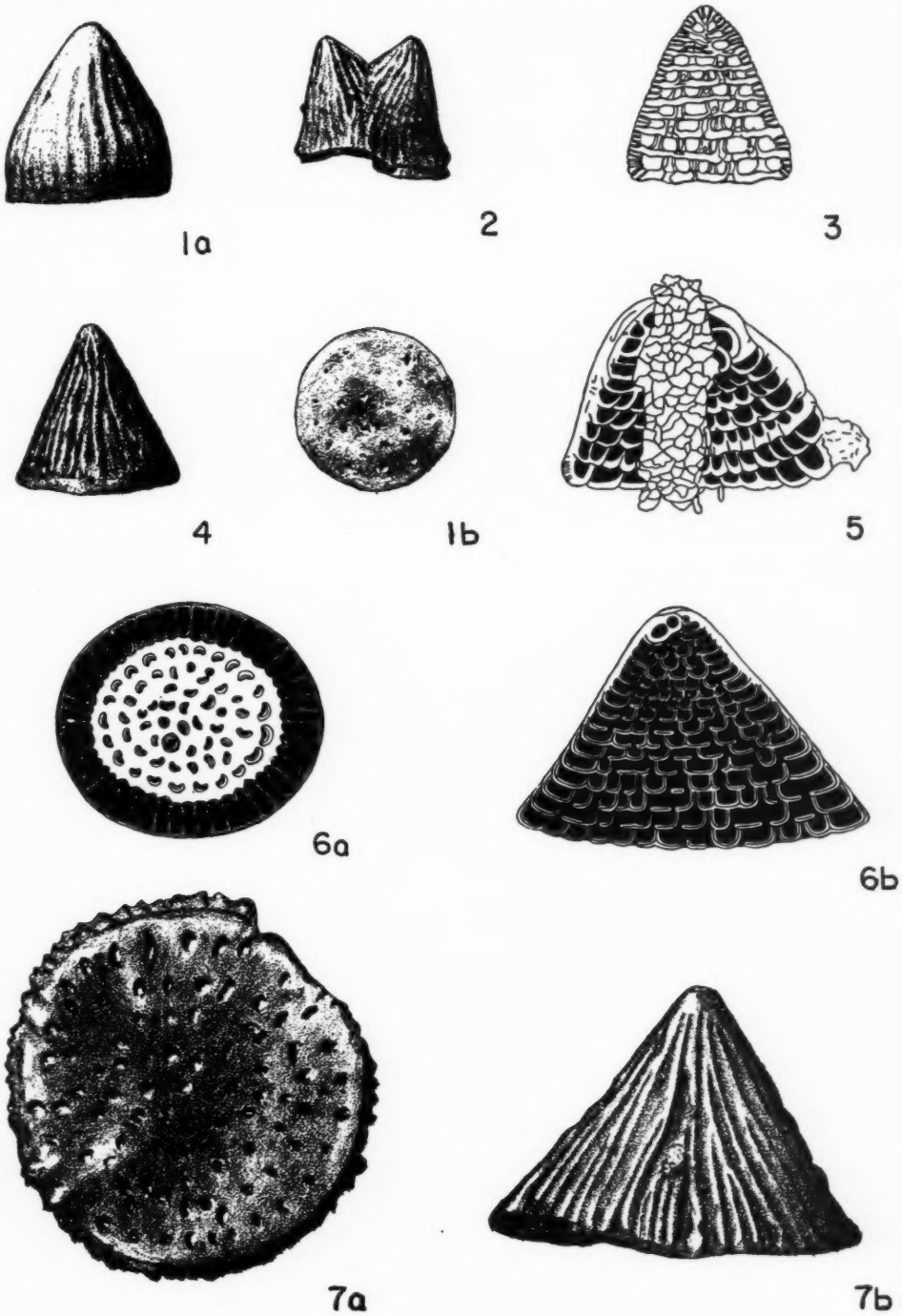
EXPLANATION OF FIGURES 1–7

FIGS. *1–4—Ferayina coralliformis* Frizzell, new species. *1a, 1b*, paratype; diameter, 0.31 mm. *2*, paratype showing teratological development of double apex; diameter, 0.29 mm. *3*, paratype; vertical section showing trochoid initial spiral, subsequent uniserial chambers, tube-pillars, and coarse perforations of outer wall. Note pores at base of tube-pillars in first to sixth uniserial chambers. Diameter, 0.31 mm. *4*, side view of holotype; diameter, 0.30 mm.

FIG. *5—Preverina galea* (Silvestri), tracing of original figure (from Ellis and Messina, 1940); diameter, 0.95 mm.

FIG. *6—Chapmanina gassinensis* (Silvestri), after Silvestri (1905, p. 479, text figures 5, 4). *6a*, horizontal section; diameter, 1.3 mm. *6b*, vertical section; diameter, 1.7 mm. (Compare details of wall structure with diagrammatic sketch of figure 20.)

FIG. *7—Ferayina peruviana* Frizzell, new species; holotype; diameter, 0.61 mm. *7a*, basal view. *7b*, side view.



FIGS. 1–7

comparable forms in *Orbitolina* were not viable at the adult stage of growth.

FERAYINA PERUVIANA Frizzell, new species
Figures 7 a–b

Description:—Test free, small, conical, strongly resembling a minute solitary coral. Apex of test acute, base flat; diameter/height ratio 127%. Test sculptured with numerous thread-like longitudinal ribs with wide interspaces, which increase in number by branching and rarely by intercalation; more than 55 ribs on last chamber. Wall moderately thin. Apertures extremely numerous, circular to subcircular, tube-pillars visible as thickenings when septum is moistened; apertures arranged in about five concentric circles, less regularly concentric at center; count of one quadrant resulted in an estimate of 100-120 apertures for the last chamber. Details of the interior are unknown. Dimensions of holotype: height, 0.48 mm.; diameter, 0.61 mm.

Type locality.—Department of Piura, Peru, between the towns of Talara and Negritos on road to airport; Square Mile 3-N-3, 5,230 feet north and 4,510 feet east of the southwest corner of the square mile (Bosworth, 1922, folders I and II, opposite pages 7 and 25; Square Mile 3-N-3 is between lines 2 and 3 north and 2 and 3 east on Bosworth's grid). The locality is about 300 feet west along the ravine (*quebrada*) that intersects the road and railroad at the cross and statue of a monkey. The sample consists of weathered brown shale, belonging to the middle of the Talara shale ("Rica zone" of local usage). Larger Foraminifera of the genera *Operculinoides*, *Amphistegina*, and *Helicolepidina* are associated with an abundant and characteristic smaller foraminiferal fauna. Collected by D. L. Frizzell and H. E. Frizzell, August 29, 1942.

Disposition of type.—The holotype has been deposited in the Cushman Laboratory for Foraminiferal Research, Sharon, Massachusetts.

Comparisons.—The single known specimen of *Ferayina peruviana* is similar to *F. coralliformis*, but is considerably larger and has a larger angle of the test. Its longitudinal ribs are finer, more widely spaced, and more numerous, and increase in number by branching rather than by intercalation. In addition, *F. peruviana* has more numerous apertures than in the genotype.

Stratigraphic position.—The Talara shale has been subdivided by local paleontologists into three foraminiferal divisions. The lowest of these is characterized by *Trochammina samanica* W. Berry (1928, p. 399, text figs. 18 a–d). It contains in its lower part the discocyclinid species *Pseudophragmina* (*Proporocyclina*) *peruviana* (Cushman), a species accepted by Vaughan (1945) as of middle Eocene age. The next higher division contains a horizon with *Helicolepidina august-tobleri* (W. Berry) (1932, pp. 1, 8, text figs. 1, 7). The holotype of *Ferayina peruviana* came from these beds and exact level. Inasmuch as *Helicolepidina* generally is considered to be diagnostic of upper Eocene age, and because there is a marked change from the fauna of the lower level, the division containing *F. peruviana* is regarded as belonging to the lower part of the upper Eocene succession. (See Wiedey and Frizzell, 1940, and Stainforth, 1948, for stratigraphic data on the area.)

Remarks.—*Ferayina peruviana* is an extremely rare species. In six years of micropaleontological routine and research work in northwestern Peru, dealing with thousands of Talara shale samples, I encountered the species but once. Nevertheless in the light of morphological studies of *F. coralliformis*, the South American form can be described with confidence. Moreover, the recognition of a second species of *Ferayina* confirms the validity and emphasizes the unity of the genus.

Genus CHAPMANINA Silvestri,
1931 (*emend.*)

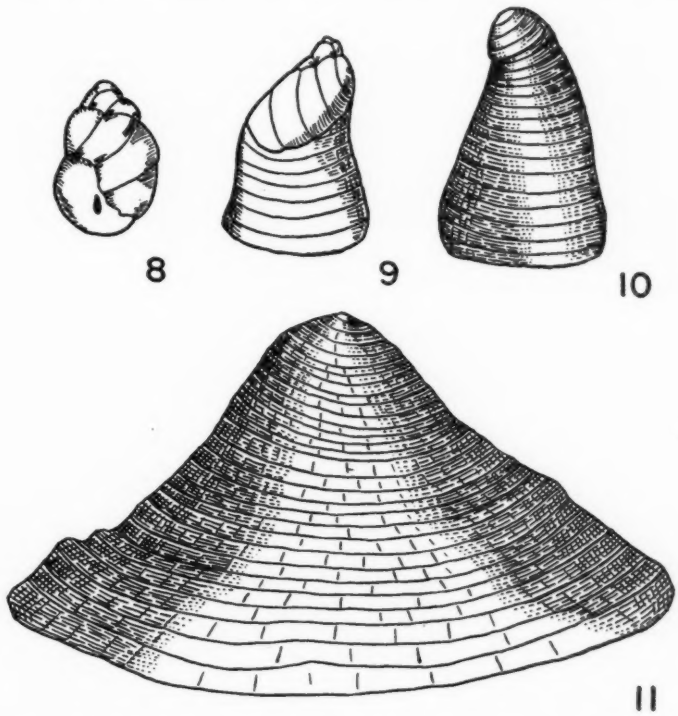
Chapmania SILVESTRI and PREVER, 1904, *in* Silvestri, Riv. Ital. Sci. Nat., Boll. Nat., anno 24, no. 12, p. 117, text figs. 1–3 (*not* Monticelli, 1893, Naturalista Siciliano, vol. 12, p. 208).

"*Archapmanoum*." RHUMBLER, 1913, Plankton-Expedition, Ergeb., Bd. 3, L, C, Teil 2, pp. 391–392 (*invalid*).

Chapmanina SILVESTRI, 1931, Soc. Geol. Ital., Boll., vol. 30, pp. 63–66.

Genotype (*by substitution*).—*Chapmania aegyptiensis* (Chapman) of Silvestri (*not Patellina egyptiensis* Chapman, genotype of *Dictyoconus* Blanckenhorn) = *Chapmania gassinensis* Silvestri.

Diagnosis.—Test medium small (1.65 mm. maximum in genotype), free, conical, with flat or convex base; uneroded specimens completely covered by calcareous secondary deposits (Halkyard, 1918); eroded specimens and sections (Silvestri) show test with apical chambers in a greatly reduced trochoid spiral, followed by a uniserial series of low chambers extending in the direction of the axis of the initial coil; each chamber with a peripheral row of closed chamberlets formed by infolding of the septum and separated from the central portion by an upward flexure into a marginal trough; chamberlets sometimes incompletely subdivided (see figure 6a); wall of test calcareous (apparently perforate in early chambers), septa double and with intraseptal spaces (evidently interspaces and not true canals); apertures multiple, restricted to central undivided part of chamber, consisting of circular to semilunar openings, the surrounding septum invaginating to form funnel-shaped tube-pillars; tube-pillars connecting with preceding septum but usually open on one side; communication of protoplasm apparently in large part through intra-septal spaces, although most tube-pillars probably were functional apertures and Silvestri reported pores connecting chamberlets and central cavity.



FIGS. *8–11*—Sketches showing progressive reduction of initial spiral in the *Dictyoconus* lineage, drawn to same scale of enlargement (modified from published sources). *8*, *Arenobulimina* stage; diameter, ca. 0.8 mm. *9*, *Lituonella* stage; diameter, ca. 1.1 mm. (Details of septation at the apex probably are incorrect.) *10*, *Coskinolina* stage; diameter, ca. 1.3 mm. *11*, *Dictoyconus* stage; diameter, ca. 5.1 mm.

Range.—Middle? and upper Eocene of southern Europe.

Content of genus.—Only *Chapmanina gassinensis* (Silvestri) can be referred with certainty to the genus. "*Chapmania*" *sertata* Silvestri (1929, p. 21, pl. 3, fig. 9), from the middle Eocene of Italy, is based on a tangential section in matrix. Evidence is not conclusive that it belongs to *Chapmanina*. "*Chapmania*" *galea* Silvestri, from the Italian middle Miocene, belongs to the

new genus *Preverina*. "*C.*" *kiliani* Prever and *silvestrii* Prever (Prever and Silvestri, 1905, p. 470) are *nomina nuda* for Cretaceous species that have been placed in the arenaceous genus *Orbitolinopsis* Silvestri (1932, p. 159).

Nomenclature.—Silvestri and Prever proposed the monotypic genus *Chapmania* for Italian specimens which they misidentified with *Patellina egyptiensis* Chapman. That species is the genotype by subsequent designation of *Dictyoconus* Blanckenhorn. In the following year, Silvestri recognized the distinctness of the Italian form, renaming it *Chapmania gassinensis*. Later, Rhumbler proposed a "modernized" system of nomenclature to replace the conventional Linnean system, by means of which classificatory position and geographic range were to be shown in generic and specific names. *Chapmania gassinensis* was emended by Rhumbler to *Archapmanoum gassinicoum*. In 1931, Silvestri pointed out that *Chapmania* is preoccupied, and renamed the genus *Chapmanina*. Three problems are posed by these actions: The identity of *Chapmania* Silvestri and Prever; the validity of *Archapmanoum* Rhumbler; and the validity and identity of *Chapmanina* Silvestri.

The biological identity of *Chapmania* Silvestri and Prever is obvious. It is distinct from *Dictyoconus egyptiensis* (Chapman). Opinion 168 of the International Commission on Zoological Nomenclature (1945) specifies that a species (not a specific name) is the type of a genus. It further stipulates that a type species (whether originally or subsequently designated) is assumed to be correctly identified, unless there is evidence to the contrary. Unfortunately, a decision by the Commission is required to validate a genus, such as *Chapmania*, which is based upon an erroneously determined species. A petition is being prepared for presentation to the International Commission on Zoological Nomenclature, requesting that the type of *Chapmania* Silvestri and Prever (not Monticelli) be fixed as *C. gassinensis*. This action is required to preserve the genus *Chapmanina* Silvestri in its current sense.

The unavailability of Rhumbler's "modernized names," including *Archapmanoum*, is shown by Opinion 72 of the International Commission on Zoological Nomenclature (1922). Although that Opinion deals specifically with a similar and earlier proposal by Herrera, it contains a discussion of Rhumbler's (1910, 1912) nomenclatural system. Denial of Herrera's "zoological formulae" therefore demands rejection of Rhumbler's "modernized names," and excludes *Archapmanoum* from consideration.

Chapmanina Silvestri was proposed as a substitute for the preoccupied *Chapmania* Silvestri and Prever, but without designation of a genotype. According to the provisions of Article 30, II, f of the International Rules of Zoological Nomenclature (Schenk and McMasters, 1936, p. 35), therefore, both names take the same type species. The name *Chapmanina* is used here, although it admittedly will remain a *nomen dubium* until the identity of *Chapmania* is established, in the belief that the International Commission on Zoological Nomenclature will not force us to reject a name that is firmly entrenched in the literature of Foraminifera.

CHAPMANINA GASSINENSIS (Silvestri)
Figures 6a–b, 20

Conulites aegyptiensis (Chapman). AIRAGHI, 1904, Soc. Ital. Sci. Nat., Atti, vol. 43, pp. 159–174; 1904, *ibid.*, vol. 43, pp. 182–188, pl. 5, figs. 1–4. (*Not Patellina egyptiensis* Chapman = *Dictyoconus*.)

Chapmania aegyptiensis (Chapman). SILVESTRI, 1904, Riv. Ital. Sci. Nat., Boll. Nat., anno 24, no. 12, pp. 117–118, text figs. 1–3; 1905, Soc. Geol. Ital., Boll., vol. 23 (1904), pp. 478–486, text figs. 1–5. (*Not Patellina egyptiensis* Chapman.)

Chapmania gassinensis SILVESTRI, 1905, Soc. Geol. Ital., Boll., vol. 23 (1904), pp. 481–482 (*name proposed in discussion, but not used formally*); 1905, Pont. Accad. Romana Nuovi Lincei, Atti, tomo 58, anno 58, pp. 130–131 (*proposed as new in formal usage, but with footnote to preceding*); 1905, Riv. Ital. Paleont., anno 11, fasc. 3, pp. 114–119, pl. 2, figs. 1–8. text figs. 1–2.—SCHUBERT, 1912, Austria, Geol. Reichsanst., Jahrb., Bd. 62, pp. 199–200, 207.—RHUMBLER, 1913, Plankton-Exped. Humboldt-Stiftung, Ergeb., Bd. 3, L, C, Teil 2, p. 392, text figs. 131 a–c.—HERON-ALLEN and EARLAND, 1918, *in* Halkyard, Manchester Lit. Philos. Soc., Mem. Proc., vol. 62, p. 106 (see *Patellina conica* Halkyard, below).—SILVESTRI, 1923, R. Accad. Naz. Lincei, Cl. Sci. Fis. Mat. Nat., Rend., ser. 5, vol. 32, 2d sem., pp. 88–90.—CHECCHIA-RISPOLI, 1925, *ibid.*, Mem., ser. 6, vol. 1, p. 7, pl. 1, fig. 7, pl. 2, fig. 1.—SILVESTRI, 1925,

Accad. Pont. Sci. Nuovi Lincei, Mem., ser. 2, vol. 8, pp. 31–49, text figs. 1–4, pl. 1, figs. 1–5.—CUSHMAN, 1927, Cushm. Lab. Foram. Res., Contr., vol. 3, pt. 1, p. 43, pl. 6, fig. 2.—SILVESTRI, 1927, Riv. Ital. Pal., vol. 33, pp. 26, 30, pl. 2, fig. 14.—CUSHMAN, 1928, Cushm. Lab. Foram. Res., Sp. Publ. no. 1, pl. 23, fig. 15.—DAVIES, 1930, Roy. Soc. Edinburgh, Trans., vol. 56, pp. 485–489, 500.—GALLOWAY, 1933, Man. Foraminifera, p. 318, p. 29, fig. 2.

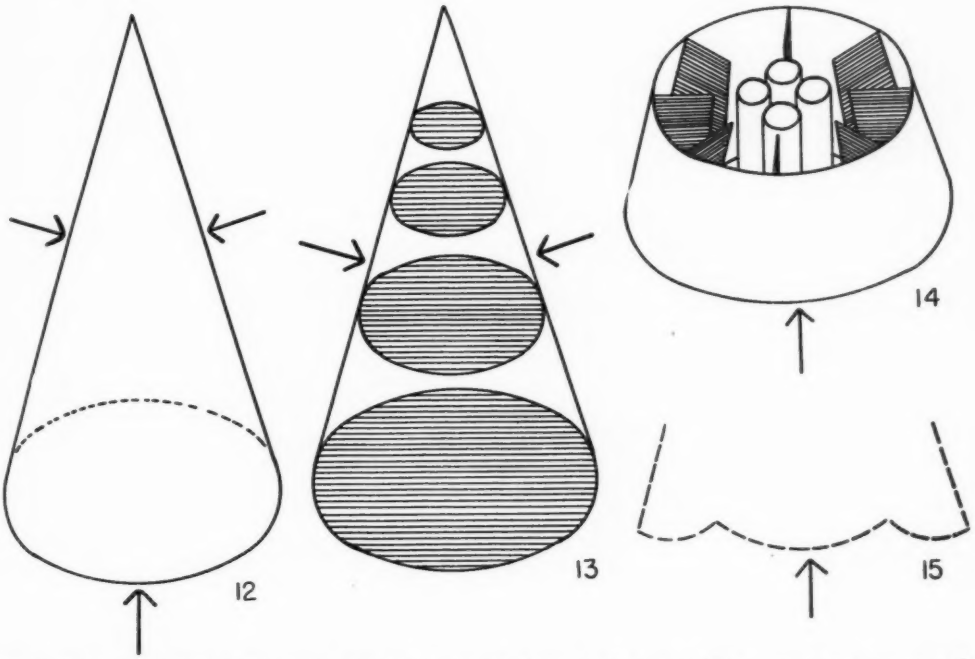
Genus PREVERINA Frizzell, new genus

Genotype.—*Chapmania galea* Silvestri.

Diagnosis.—Test calcareous-perforate, small (about 1 mm. diameter), free, conical, with flat or slightly convex base; consisting of an initial trochoid spiral followed by a series of low uniserial chambers extending in the direction of the axis of the trochoid coil; wall and septum single; septa of uniserial chambers invaginating into a series of about four or five concentric rows of chamberlets, with vestigial tube-pillars developed in the central parts; apertures apparently consist of canal-like tubules penetrating the greatly reduced tube-pillars.

Range.—Oligocene? to middle Miocene of Italy.

Comparisons.—*Preverina* differs from *Chapmanina* in the single wall and absence



FIGS. *12–15*—Structural diagrams showing external forces acting on hollow cone and supporting mechanisms to resist them. Arrows show directions of forces. *12*, cone without reinforcement. *13*, lateral forces resisted by series of internal plates. *14*, frustum of cone between plates, showing pillars and buttresses preventing collapse of plates. *15*, cross section of base of cone: arches in plate give further reinforcement against vertical forces.

Chapmania sp., DE CIZANCOURT, 1933, Service Géol. de Pologne, Bull., vol. 7, livr. 4, p. 764, pl. 34, fig. 16.

"*Archapmanoum gassinicoum*." RHUMBLER, 1913, Plankton-Exped. Humboldt-Stiftung, Ergeb., Bd. 3, L, C, Teil 2, p. 392, text figs. 131 a–c (*invalid*).

Patellina conica HALKYARD, 1918, Manchester Lit. Phil. Soc., Mem. Proc., vol. 62, pt. 2, no. 6, p. 106, pl. 6, fig. 7. pl. 8, figs. 6–7.

Chapmanina gassinensis (Silvestri). SILVESTRI, 1931, Soc. Geol. Ital., Boll., vol. 50, pp. 63–66, pl. 1, figs. 1–2; 1932, Pont. Accad. Sci. Nuovi Lincei, Mem., ser. 2a, vol. 16, pp. 383–385, pl. 2, fig. 7.—DAVIES, 1939, Roy. Soc. Edinburgh, Trans., vol. 59, pt. 3, pp. 777–778, text fig. 1a.—CUSHMAN, 1940, Foraminifera, etc., ed. 3, p. 279, pl. 40, figs. 12–13; 1948, *ibid.*, ed. 4, p. 310, pl. 40, figs. 12–13.

of intra-septal spaces. It is distinguished as well by the relatively larger initial spiral, and by the greater number of rows of chamberlets. *Preverina* is separated from *Ferayina* by its development of chamberlets and reduction of the tube-pillars.

Content of genus.—Only the genotype is known.

Remarks.—"*Chapmania*" *galea* Silvestri was described from a single vertical section, the details of which are obscured in part by a replacement with crystalline calcite. Although no specimens have been available for study, Silvestri's careful draftsmanship shows the relationship of the genus to the other members of the subfamily. The genus is named in honor of the Italian paleontologist P. L. Prever.

PREVERINA GALEA (Silvestri)
Figure 5

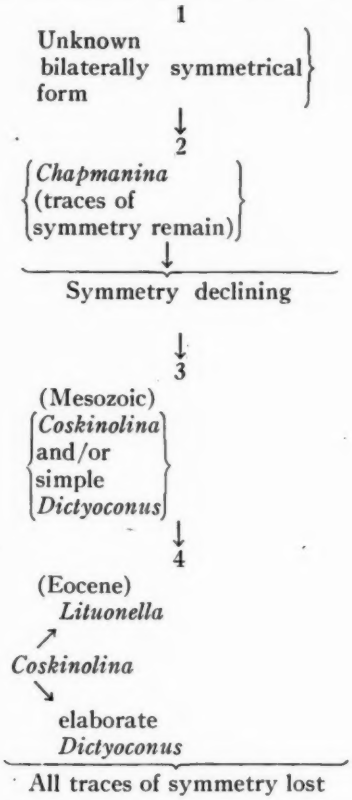
Chapmania galea SILVESTRI, 1923, R. Accad. Naz. Lincei, Atti, Rend., Cl. Sci. Fisiche, Mat. Nat., ser. 5, vol. 32, sem. 2, no. 3–4, p. 90, text fig. 1; 1925, Accad. Pont. Sci. Nuovi Lincei, Mem., ser. 2, vol. 8, pp. 40–41, text fig. 8 (*original figure reprinted*).

CONVERGENT EVOLUTION OF STRUCTURAL REINFORCEMENTS IN *CHAPMANINA* AND *DICTYOCONUS*

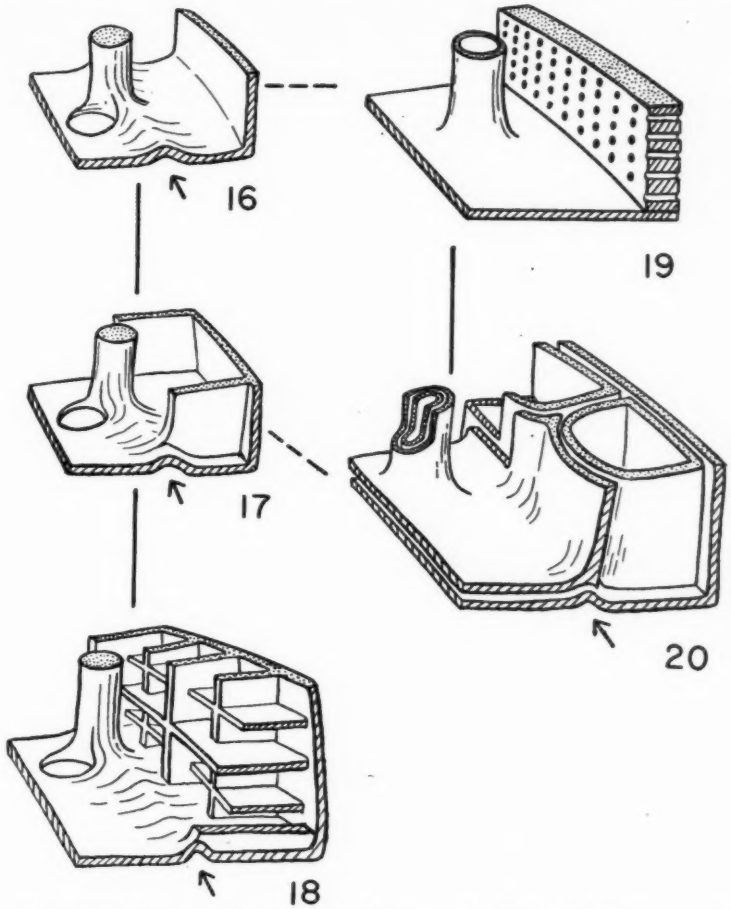
The problem

Chapmanina Silvestri and *Dictyoconus* Blanckenhorn (1900, p. 419) have been confused by various workers, first as to their identity and later as to their structure and affinities, since the time of their proposal. Both are conical forms that begin as trochoid spiral tests, continuing through their major growth in a uniserial pattern. Both have multiple apertures and associated cylindrical pillars, and both show marginal radiating septation. Their fundamental distinction, however, is shown by the calcareous wall of *Chapmanina* and the arenaceous composition of *Dictyoconus*, as well as in details of the pillars and of the marginal septation. The separation has been generally accepted, and no discussion of their affinities would be needed were it not for a recent revival of the confusion.

Davies (1939), whose superb studies of the gross morphology of *Dictyoconus* and other large Foraminifera have contributed greatly to our knowledge, was able to ignore both stratigraphic anachronism and established implications of wall structure, considering but discarding the likelihood of "an extreme case of convergence," in arriving at the following developmental series:



Ignoring the implicit chronological incongruity, of which Davies was well aware, one finds two untenable assumptions involved: First is the inference that possession of an extramural crust "links *Chapmanina* to bilaterally symmetrical forms" (1939, p. 777). This crust, better termed *secondary deposits*, is to be found in all calcareous-perforate Foraminifera of which I have examined thin sections. These deposits, which occur internally as well as externally, are easily explained: The foraminifer lives simultaneously inside and outside the test, filling and covering it. Deposition of calcium carbonate is not restricted to the last formed chamber, but takes place throughout the entire organism. Consequently, the development of each new chamber is accompanied



FIGS. *16–20*—Structural diagrams showing development of pillars and buttresses in *Dictyoconus* lineage (figures *16–18*) and *Chapmanina* lineage (figures *19–20*) (figures *16–18* drawn according to interpretations of Davies and of Cushman). Sketches oriented to show outer wall at right and septum at base; arrow indicates flexure separating central shield from marginal trough.

16, Lituonella; pillar developed beside aperture and partly surrounding it, marginal trough present. *17, Coskinolina;* simple buttresses added to mechanism of *Lituonella*. *18, Dictyoconus;* lateral intersecting buttresses and subsidiary transverse plates further subdividing interspaces.

19, Ferayina; tube-pillar developed, wall simple and distinct from septum. *20, Chapmanina;* peripheral chamberlets added to form buttressing structures; wall double, with intra-septal spaces. (This reconstruction of wall structure is clearly evident from the details of figures *6a* and *6b*.)

by thickening of the wall of earlier chambers. Whether these secondary deposits preserve the sutural pattern, as in *Operculina* (see Carpenter, 1862), or, as in *Chapmanina* and *Ferayina*, obscure the plan of growth, is a trait of the genus or species involved. It may be mentioned in passing that Davies indicated the proloculum incorrectly (1939, fig. 1a). He selected the youngest and largest visible chamber of the spiral as shown in thin section, whereas the actual proloculum cannot be demonstrated in that figure.

The second incorrect assumption is that arenaceous Foraminifera are to be regarded as identical with the "porcellanous" (calcareous-imperforate) forms—an inference supported only by chemical analysis and negated by his own important discovery that the supposed arenaceous test of *Gunteria* Cushman and Ponton (1933, p. 25) is basically calcareous-perforate. Glaessner (1945, p. 65) has already pointed out the

chemical similarity between secreted calcium carbonate and the adventitious calcareous grains of certain arenaceous Foraminifera. Galloway's (1933, p. 19) postulated evolutionary development of the wall of the test seems to be well substantiated in its main thesis that arenaceous composition is an end product. Arenaceous forms have developed from naked, chitinous, calcareous-perforate, and calcareous-imperforate stocks. Arenaceous composition is not a valid single basis for classification, nor can it be restricted to affiliation with the calcareous-imperforate groups.

Cushman (1937) has applied Davies' interpretations of gross morphology in *Dictyoconus* and its allies to his own phylogenetic-morphological studies, arriving at a lineage that is remarkably parallel to the rotaliine—*Ferayina*—*Chapmanina* series. This parallelism is a response, under genetic control, to structural requirements.

Comparison of lineages

Dictyoconus.—Cushman (1937, pp. 3, 171) postulated a lineage of the valvulinid genera *Arenobulimina* (Cushman, 1927, p. 80)—*Lituonella* (Schlumberger, *in* Schlumberger and Douvillé, 1905, p. 297)—*Coskinolina* (Stache, 1875, p. 335)—*Dictyoconus* (see figures 8 to 11 and 16 to 18). All of these arenaceous forms except *Arenobulimina* were placed in the Ataxophragmiinae by Cushman, that genus presumably having been the radicle from which several stocks evolved. Although the subfamily Ataxophragmiinae has been dropped from Cushman's latest classification (Cushman, 1948), it is retained here as a convenient and natural subdivision of the family Valvulinidae.

Evolution in the *Dictyoconus* lineage was from a simple trochoid spiral, in *Arenobulimina*, to a reduced initial trochoid spiral with subsequent uniserial chambers in *Lituonella*. The latter is characterized by multiple apertures and associated pillars, as well as by a differentiation of the septum into a central shield and marginal trough (figure 16). Further reduction in size of the initial trochoid spiral and increase of the uniserial portion resulted in the conical test of *Coskinolina*. At the same time, transverse plates were added across the marginal furrow in each later chamber (figure 17). The end member of this series, *Dictyoconus*, is characterized by a greatly reduced initial spiral. The transverse plates are subdivided into a grid-like pattern by the addition of secondary transverse plates and primary and secondary lateral plates (figure 18).

Several trends are involved in this sequence: (1) change from trochoid to uniserial pattern, with progressive reduction of size of the initial spiral; (2) multiplication of apertures; (3) development of pillars; (4) differentiation of septum into central shield and marginal trough; and (5) addition of transverse and lateral plates at the periphery. The recently proposed Lower Cretaceous genus *Coskinolinoides* Keijzer (1942) apparently is an offshoot of the lineage, possibly from *Coskinolina* by loss of the pillars.

Chapmanina.—The lineage of the rotaliid foraminifer *Chapmanina* is believed to start with an unidentified rotaliine ancestor consisting of a simple trochoid spiral. Addition of uniserial chambers to the ancestral coil, with reduction of the initial spiral, resulted in the conical shape of *Ferayina*. Multiple apertures were added in the form of tube-pillars (figure 19). Development into *Chapmanina* involved a further reduction of the initial spiral. At the same time the perforate wall was lost, having been displaced by the septum. Circulation of protoplasm then could be permitted only by the development of a double septum with intraseptal spaces. Transverse marginal chamberlets were formed by invagination of the inner septal wall, and the septum became differentiated into a central shield and ring of chamberlets that may be considered as forming a marginal trough (figure 20).

Trends similar to those in the *Dictyoconus* series are present: (1) change from trochoid to uniserial pattern, with progressive reduction in size of the initial spiral; (2) multiplication of apertures; (3) development of tube-pillars analogous to the pillars of the arenaceous lineage; (4) differentiation of septum into central shield and marginal trough; (5) development of peripheral chamberlets comparable to the marginal divisions in the *Dictyoconus* series; and (6)

origin of an intraseptal circulatory system. The position of *Preverina* in this lineage is obscure, but that genus probably is divergent and not in the direct evolutionary series of *Chapmanina*.

Structural mechanisms for reinforcing a hollow cone against external forces

A hollow cone under external pressure must withstand forces normal to the base and to the sides (figure 12). Lateral forces can be resisted by means of plates within the cone and parallel to the base (figure 13). Vertical forces, however, demand additional support to prevent collapse of these plates. Support of the plates may be by means of buttresses, pillars, arching of the plates themselves, or by a combination of all three methods (figures 14, 15).

Chapmanina and *Dictyoconus* developed adequately reinforced uniserial conical tests by the same means: septal plates opposing lateral stresses; a combination of pillars, buttresses, and arches preventing collapse of the septa (figures 16 to 20). The first step in each lineage was addition of uniserial chambers, with the acquisition of pillars. Next, radial buttresses developed. Arching of the septal face, however, was effected in an earlier stage in the *Dictyoconus* lineage. That series, too, reached a stage of greater structural support by means of a pigeonhole arrangement of subsidiary buttresses and plates.

The supporting structures of *Chapmanina* and *Dictyoconus* are *functionally homologous*. That is, they served an identical purpose in counteracting external forces. They are, however, *physiologically and anatomically analogous*. They are morphologically distinct and were formed by different physiological processes.

All of the supporting structures of *Chapmanina* and its allies originated in the septum and its modification by bending (of the lower septal element to form the marginal trough and central shield) or invagination (resulting in the peripheral chamberlets and tube-pillars). Development appears to have been from a *plane of secretion* in the outer part of the accumulation of protoplasm that formed each new chamber. Bending and invagination of this plane resulted in the surfaces that make up the supporting mechanisms of the test. (I cannot determine whether the double septum was secreted as a unit or whether, as in the nummulitids, it was deposited as a single layer. Logically, the latter should be the case. If so, each new chamber was laid down complete, with top and bottom layers, the top layer combining with the bottom layer of the preceding chamber to form a double septum with a contained intra-septal space.)

The supporting structures of the *Dictyoconus* series, in contrast, were built up grain by grain from adventitious material collected by the pseudopodia and carried into position by streams of protoplasm. Except for the arching of the septal face, they were not formed as modifications of the septum. Deposition of internal skeletal elements appears to have been that of selective protoplasmic current action within the cell, transporting and dropping extra-cellular detritus at predetermined places within the test. Pillars were built up beside the apertures rather than around them, and buttresses apparently were formed as walls that are unsupported at their inner ends. The effect is of masonry carried on within the cell, as opposed to the folded plane of secretion suggested for *Chapmanina*.

The lineages of *Dictyoconus* and *Chapmanina* are unrelated foraminiferal stocks that evolved similar shapes through the development of mechanically identical supporting structures. They reached the form of hollow cones by adopting the only mechanisms for withstanding external forces that would at the same time allow adequate space for protoplasm within the test. This explanation does not involve any direct environmental control in initiating changes, nor does it postulate any inherent orthogenetic principle. The requirements of the environment were such that a conical test could exist only if adequately reinforced against external stresses. Therefore only mutations satisfying this rigid requirement could survive and reproduce. Evolution of a conical form was directed by the environment, but progressed only through changes that were physiologically possible to the organism. Even then, a high degree of adjustment to environment was required. *Dictyoconus* and its allies had this optimum adjustment, as shown by the considerable

number of genera, species, and individuals. Their mechanisms were sound, and they flourished. The *Chapmanina* series, in contrast, never became well established. Its members are extremely rare, with very few species and genera known. Although its structure allowed the attainment of conical shape, the ultimate adjustment was not completely successful.

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FERAYINA IN THE MIDDLE EOCENE OF VENEZUELA (FORAMINIFERA, ROTALIIDAE, CHAPMANININAE)

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ABSTRACT—*Ferayina coralliformis* Frizzell (type locality: Claiborne group, Weches formation of Smithville, Texas) is recorded from the Cuicas formation (middle Eocene) of Venezuela, and the possibility of a correlative horizon is suggested. Photomicrographs of Texan and Venezuelan specimens supplement illustrations previously published.

THE genus *Ferayina* Frizzell 1949 comprises calcareous Foraminifera with tests of conical shape, the plan of growth being obscured in external view by longitudinally sculptured secondary deposits. Apertures are multiple, arranged in concentric rows on the base (septum) of the test. Internally, the genus is characterized by a greatly reduced trochoid initial spiral, followed by an expanding series of uniserial chambers. The wall and septum are single, and the wall is coarsely perforate. The test is supported by tube-pillars formed by invagination of septa around the apertures. Some of these details are shown on plate 81, figures 1 and 2, the first photomicrographs of *Ferayina* to be published. The genus differs from *Chapmanina* Silvestri (1931, pp. 63–66) in having a single wall rather than a double wall with intra-septal spaces, in the lack of peripheral chamberlets, in the relatively greater development of the initial trochoid spiral, and in its considerably smaller size.

Ferayina ranges from middle Eocene strata to beds in the lower part of the upper Eocene stratigraphic sequence. *Ferayina coralliformis* Frizzell, the genotype, occurs rarely in the Weches formation of the Claiborne group (middle Eocene) of Texas. *F. peruviana* Frizzell is known from a single specimen from the middle faunal division of the Talara shale (lower part of the upper Eocene) of Northwestern Peru. We are now able to add a second occurrence of *F. coralliformis* in the Cuicas formation (middle Eocene) of Venezuela. (See de Cizancourt for an account of stratigraphic details.)

The localities at which the Venezuelan specimens were collected are described as follows:

1. North slope of the high valley of El Cumbe, right bank tributary of Rio Carache, about 2.2 km. in a straight line from Casa de Zinc. Sample L. 860; collected by H. de Cizancourt, 1948.

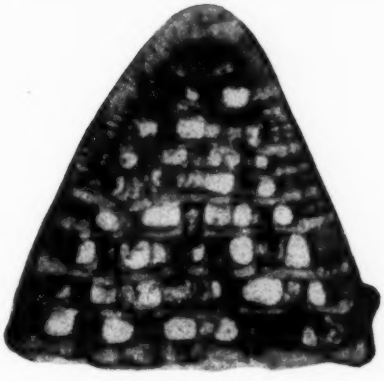
2. Pevete Valley; western slope of Cerro de los Zamures, about 900 m. north of Valle Hondo chapel. Sample A. 9361; collected by geologists of the Mene Grande Oil Company, 1948. Sample L. 793; collected by H. de Cizancourt, 1948.

3. Tucuyo Guarico road, about 3.5 km. by road south of Las Adjuntas bridge; out-

EXPLANATION OF PLATE 81

FIGS. *1*, *2*—Photomicrographs of *Ferayina coralliformis* Frizzell. *1*, Specimen in matrix section from Venezuela (Sample L. 860); height, 0.42 mm. *2*. Paratype from Smithville, Bastrop County, Texas; height, 0.29 mm. Oriented vertical section previously illustrated by camera lucida sketch (Frizzell, 1949, text figure 3). The photograph shows the opposite side of the section. It is less accurate than the sketch in details of the apex, because this side of the section passed farther from the median plane.

1



2

De Cizancourt and Frizzell, *Ferayina*

crop along road. Sample V. 833; collected by H. and M. de Cizancourt, 1939.

The specimens from the Carache region (El Cumbe and Pevete) were encountered in random thin sections of yellow limestone with algae and Foraminifera, lying above the Cuicas limonite beds. A free specimen was obtained by washing Sample A. 9361 from the limonite beds. In Sample V. 833, the specimen was found in a yellow limestone full of algae and larger and smaller Foraminifera, interbedded in a series of marls and thin sandstone beds.

Larger Foraminifera associated with *F. coralliformis* in the Venezuelan section are *Nummulites* (*Operculinoides*) *jennyi* (Barker), *N.* (*Operculinoides*) *oliveri* (Cushman), *Lepidocyclina* (*Polylepidina*) *antillea* Cushman, *Linderina floridensis* Cole, and *Helicostegina* sp. (identifications by M. de C.). These indicate middle Eocene age, especially *N. jennyi*, *N. oliveri*, and *L. antillea*, a position substantiated by field relationships.

Comparison of the best Venezuelan specimen (Sample L. 860) with paratypes of *F. coralliformis* is summarized in Table I. Except for the slightly larger size of the former, a close agreement was noted.

Current knowledge of the vertical range of *Ferayina* and its species is not sufficiently extensive to warrant their use in attempts at exact correlation. Nevertheless, these highly specialized forms probably have limited stratigraphic occurrence. If so, a correlative horizon eventually may be established between the Gulf Coast and the southern Caribbean area on the basis of *F. coralliformis*. Although the rarity of individuals limits the practical use of Chapmaninine species as guide fossils, their presence should prove a more valid clue to synchrony of beds than would forms with more abundant (and hence less rapidly evolving) populations.

TABLE I.—COMPARISON OF VENEZUELAN SPECIMEN (SAMPLE L. 860; PLATE 81, FIGURE 1) WITH PARATYPES OF *Ferayina coralliformis*.

	Paratypic suite	Venezuelan specimen
Height	0.36 mm. (maximum)	0.42 mm.
Angle of test (measured from photomicrograph)	50°–52° (figured paratype)	57°
Number of uniserial chambers	10 (maximum)	ca. 11
Diameter/height ratio	80%–132% (typically 80%–90%)	79%
Number of tube-pillars in section	5 (last chamber; figured paratype)	5 (penultimate chamber)

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(SUPPLEMENTS AND CORRECTIONS FOR THE PERIOD 1931 TO 1947)

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IN THE following bibliography of the Foraminifera a total of 152 titles of papers dealing partly or exclusively with Foraminifera are listed, which had been omitted or overlooked in former annual bibliographies for the years 1931 to 1947 inclusive. There are supplemented for the year 1931: 3, for 1932: 1, for 1933: 4, for 1936: 3, for 1937: 6, for 1938: 2, for 1939: 16, for 1940: 19, for 1941: 15, for 1942: 17, for 1943: 11, for 1944: 14, for 1945: 18, for 1946: 22, and for 1947: 1 title. Only a few of them contain descriptions of new species or varieties of Foraminifera. The majority deal with stratigraphic occurrences of single genera or species, or of foraminiferal assemblages and are, therefore, valuable from a paleogeographic point of view.

The supplements to the index to new Foraminifera list 1 genus, 18 species, 15 varieties (or subspecies), 3 nomina nova, 4 homonyms (of which one is here renamed) and 8 forms to which the nomenclatura aperta was applied. These new forms have been erected between 1939 and 1946 and had been overlooked or were unknown to the compiler when the materials for the respective annual bibliography and index were assembled.

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Elphidium hanzawai Asano, Jour. Geol. Soc. Japan, vol. 46, No. 551, p. 426, text figs. 3, 4. Pliocene, Oga Peninsula, Japan.

Gaudryina (*Pseudogaudryina*) *oga* Asano, *ibid.*, vol. 46, No. 551, p. 425, text fig. 2. Pliocene, Og Peninsula, Japan.

Gaudryina yabei Asano, *ibid.*, vol. 46, No. 551, p. 425, text fig. 1. Pliocene, Oga Peninsula, Japan.

Pseudogaudryina, see *Gaudryina*.

(Note: The exact title of this paper by Asano is found in Jour. Paleontology, vol. 16, No. 4, 1942, p. 490, No. 16.)

SUPPLEMENT FOR 1940

Fibrcsphaera, gen. nov. Wanner. Paleont. Zeitschr., vol. 22, p. 92. Eocene, France. No genotype designated. (Note: Reference is made by Wanner to the fibrospheres described by de Lapparent in Bull. Soc. géol. France (4), vol. 24, 1924, p. 617, for which this new genus is proposed. The title of Wanner's paper is found in Jour. Paleontology, vol. 17, No. 4, 1943, p. 408).

SUPPLEMENT FOR 1941

In F. and G. Kahler's paper, cited in Jour. Paleontology, vol. 22, No. 2, 1948, p. 203, No. 203, the following new species were erected:

Pseudoschwagerina alpina F. and G. Kahler, Palaeontogr., vol. 92, Abt. A, p. 86, pl. 10, figs. 1, 2; pl. 11, fig. 5. Lower Permian, Carinthian Alps.

—— *cheni nom. nov.* F. and G. Kahler, *ibid.*, vol. 92, Abt. A, p. 73. New name for: *Schwagerina fusulinoides* Chen., 1934, (non Schwellwien, 1892). Palaeont. Sinica, (B), vol. 4, No. 2, p. 94, pl. 14, figs. 1–4; pl. 15, fig. 7. Permian, China.

—— *citriformis* F. and G. Kahler, *ibid.*, vol. 92, Abt. A, p. 90, pl. 10, fig. 6. Lower Permian, Carinthian Alps.

—— *elegans* F. and G. Kahler, *ibid.*, vol. 92, Abt. A, p. 91, pl. 10, figs. 3, 4. Lower Permian, Carinthian Alps.

—— *lata* F. and G. Kahler, *ibid.*, vol. 92, Abt. A, p. 93, pl. 11, figs. 1, 2. Lower Permian, Carinthian Alps.

—— *leei nom. nov.*, F. and G. Kahler, *ibid.*, vol. 92, Abt. A, p. 73. New name for: *Schwagerina fusulinoides* Lee, 1927, (non Schellwien, 1892), Paleont. Sinica, (B), vol. 4, No. 1, p. 118, pl. 22, figs. 6–17. Permian, China.

—— *sp.* F. and G. Kahler, *ibid.*, vol. 92, Abt. A, p. 78. For: *Schwagerina princeps* Schellwien, 1892, Paleontogr., vol. 44, p. 258, pl. 12, figs. 5–7, 9; pl. 22, figs. 4–7.

—— *sp.* F. and G. Kahler, *ibid.*, vol. 92, Abt. A, p. 79. For: *Schwagerina princeps* Lee, 1927 (non Schellwien, 1892), Paleont. Sinica, B, vol. 4, Fasc. 1, p. 122, pl. 24, figs. 4–6.

—— *sp.* F. and G. Kahler, *ibid.*, vol. 92, Abt. A, p. 79. For: *Schwagerina princeps* Yabe, 1906, (non Schellwien, 1892), A Contr. to the genus *Fusulina* etc., p. 2, pl. 1, fig. 1.

SUPPLEMENT FOR 1943

Camerina (*Nummulites*) *pseudoparva* Méhes, Magy. Kir. Földt. Int. Evi., p. 204, text figs. 1–3. Eocene, Hungary.

According to C. A. Hoare and C. D. Ovey, Zoological Record, vol. 83, Sect. 2 (Protozoa), 1948, pp. 29 and 97, P. Husnot in his paper on the genus *Cyphoderia*, mentioned in the preceding Bibliography (Supplement for 1943), classifies the following species and varieties of the genus *Cyphoderia* as belonging probably to the fresh water Foraminifera:

Cyphoderia euglyphoides nov. spec.
—— *trochus* var. *magna* nov. var.
—— —— var. *longicollis* nov. var.
—— —— var. *umbonata* nov. var.
—— *crassa* nov. spec.
—— —— var. *hians* nov. var.
—— —— var. *falciformis* nov. var.
—— *communis* var. *magna* nov. var. (Homonym of *Cyphoderia trochus* var. *magna*, *ut supra*).
—— —— var. *mamillaria* nov. var.
—— —— var. *acuminata* nov. var.
—— —— var. *strangulata* nov. var.
—— —— var. *tubulosa* nov. var.

All these new forms are from Saint-Brieuc, France. (Note: The writer was unable to obtain a copy of Husnot's work).

SUPPLEMENT FOR 1944

Nummulites agostensis Llueca, Bol. Soc. Espana Hist. Nat., vol. 42, p. 513, pl. 47, figs. 1–10, Lutetian, Spain.

—— *gaonensis* Llueca, *ibid.*, vol. 42, p. 514, pl. 48, figs. 1–3. Lutetian, Spain. (*Cave: Nummulites praelucasi* H. Douvillé, 1926 var. *ganensis* Arni, 1939.)

SUPPLEMENT FOR 1946

Ammobaculites cassis (Parker, 1870) var. *inflatus* Stschedrina, Arctic Sci. Research Inst., Trans., Drifting Exped. . . . Icebreaker "G. Sedov" 1937–1940, vol. 3, (Biol.), p. 141, pl. 3, fig. 14; text fig. 1(1–10). Recent, Arctic Ocean.

Astrorhiza limicola Sandahl, 1858, var. *arenifera* Stschedrina, *ibid.*, vol. 3, (Biol.), p. 140, pl. 1, fig. 1; pl. 2, figs. 4, 6, 7. Recent, Arctic Ocean.

—— —— —— var. *sabulifera* Stschedrina, *ibid.*, vol. 3, (Biol.), p. 139, pl. 1, figs. 2, 3; pl. 2, figs. 5, 10. Recent, Arctic Ocean.

Cornuspiroides profundum Stschedrina, *ibid.*, vol. 3, (Biol.), p. 143, pl. 4, fig. 17; text fig. 17. Recent, Arctic Ocean.

Elphidium goesi Stschedrina, *ibid.*, vol. 3, (Biol.), p. 144, pl. 4, fig. 20. Recent, Arctic Ocean.

—— *gorbunovi* Stschedrina, *ibid.*, vol. 3, (Biol.), p. 144, pl. 4, fig. 21. Recent, Arctic Ocean.

Entosolenia groenlandica Stschedrina, *ibid.*, vol. 3, (Biol.), p. 144, pl. 4, fig. 19. Recent, Arctic Ocean.

—— *sigmoidella* (Cushman) var. *timmensis* Cushman and Gray, Cushman Lab. Foram. Research, Spec. Publ. No. 19, p. 30, pl. 5, figs. 34–36. Pliocene (or Pleistocene ?) California.

Globigerina groenlandica Stschedrina, Arctic Sci. Research Inst., Trans., Drifting Exped. . . . Icebreaker "G. Sedov," vol. 3. (Biol.), p. 145, pl. 4, fig. 23 Recent, Arctic Ocean.

Hyperammina bradyi nom. nov. Stschedrina, *ibid.*, vol. 3, (Biol.), p. 141, pl. 3, fig. 12. Recent Arctic Ocean.

Lagena striato-punctata Parker and Jones, 1865, var. *tricosta* Cushman and Gray, Cushman Lab. Foram. Research, Spec. Publ. No. 19, p. 21, pl. 4, fig. 5. Pleistocene(?) or Pliocene, California.

Miliolina sadko Bogdanowicz in Stschedrina, Arctic Sci. Research Inst., Trans., Drifting Exped. . . . Icebreaker "G. Sedov" . . . vol. 3, (Biol.), p. 139, pl. 3, fig. 15; text fig. 2. Recent, Arctic Ocean. (Note: This species is named *M. sadkovi* on p. 142 and p. 147.)

Trochammina karica Stschedrina, *ibid.*, vol. 3, (Biol.), p. 143, pl. 3, fig. 16. Recent, Arctic Ocean.

Dentalina sp. Cushman and Renz, Contr. Cushman Lab. Foram. Research, Spec. Publ. No. 18, p. 29, pl. 4, fig. 23. Upper Cretaceous, Trinidad.

Hauerina sp. Cushman, Cushman Lab. Foram, Research. Contr., vol. 22, p. 13. pl. 1, fig. 11. Oligocene, Mississippi.

Hyperammina ? sp. Cushman and Renz, *ibid.*, Spec. Publ. No. 18, p. 13, pl. 1, fig. 11, Upper Cretaceous, Trinidad.

Planispirina ? sp. Cushman and Gray, *ibid.*, Spec. Publ. No. 19, p. 11, pl. 2, fig. 9. Pleistocene or Pliocene, California.

Reophax ? sp. Cushman and Renz, *ibid.*, Spec. Publ. No. 18, p. 14, pl. 1, figs. 14, 25. Upper Cretaceous, Trinidad.

NOMENCLATURAL REMARKS AND CORRECTIONS

Eponides bermudezi F. G. Keijzer, 1942, Nederl. Akad. Wetensch., Proc. vol. 45, p. 608, from the lower Oligocene of Cuba becomes a *nomen caducum* on account of synonymy with *Eponides byramensis* (Cushman, 1922) var. *campester* Palmer and Bermudez, 1941, in Palmer, 1941, Mem. Soc. Cubana Hist. Nat., vol. 15, p. 192 from the upper Oligocene of Cuba, because both authors base their names on *Eponides byramensis* (Cushman, 1922) var. *cubensis* Palmer and Bermudez, 1936 (non *Eponides cubensis* Palmer and Bermudez, 1935), Mem. Soc. Cubana Hist. Nat., vol. 10, p. 302, pl. 20, figs. 4–6.

Ptychocladia Ulrich and Bassler, 1904, Smithson. Miscell. Coll., vol. 45, p. 289, pl. 67, fig. 10 (part), fig. 13, up to now of doubtful systematic position, (formerly regarded to belong to the ctenostomatous Bryozoa) has been placed in the Foraminifera by Condra and Elias, Bull. Geol. Soc. America, vol. 55, 1944, p. 547. Upper Pennsylvanian. Family and genotype are not given by Condra and Elias.

In 1941, F. Brotzen (see Jour. Paleontology, vol. 19, 1945, p. 401, Lit. No. 129) mentioned *Chuaria wichmani nom. nov.*, a chitinous foraminifer from the pre-Cambrian Visingsö formation of Sweden. The writer, who had not seen Brotzen's paper at that time, stated on p. 410 of the Jour. Paleontology, vol. 19, (1945), that Brotzen erected a new genus. This is erroneous. Brotzen in fact introduced the new specific name *Chuaria wimani* for the Swedish forms, which are similar, though smaller in size than *Chuaria circularis* Walcott, 1899 (from the pre-Cambrian Chuar formation of the Grand Canyon) and placed the genus *Chuaria* in the Foraminifera.

Thalmann in Jour. Paleontology, vol. 15, 1941, p. 660 cited "*Rugofusulina*" Rauser-Cernoussova, 1937. This name should correctly be spelled *Rugosofusulina* Rauser-Cernoussova. Dr. M. L. Thompson (letter of January 8th, 1949) kindly rechecked the original spelling of this name. "*Rugofusulina*" in Dunbar, 1948, chapter Fusulinidae in Cushman, 1948, Foraminifera, 4th edition, pp. 159, 567, and 602 should, therefore, be corrected accordingly.

Thalmann was erroneous in claiming that *Marginulina multiplicata* Bergquist, 1942 (see Jour. Paleontology, vol. 19, 1945, p. 406) is a homonym of Bornemann, 1854. There is no specific name "*multiplicata*" erected by Bornemann within the genus *Marginulina*. The writer herewith offers his apologies to Dr. Bergquist.

NOTES ON HOMONYMS

It is with a feeling of guilt (or shame ?) that the writer has to confess the sin of having erected a homonym in *Uvigerina spinicostata* Cushman and Jarvis, 1929, var. *acuminata* Thalmann, 1939 (Lower Oligocene, Mexico). Thalmann's varietal name is already preoccupied by *Uvigerina acuminata* Hosius, 1893, Jahresber. Naturwiss. Ver. Osnabrück, No. 10, (1893–1894), p. 167, footnote, for a species from the Miocene of Westphalia. The writer takes the opportunity to propose the following new name: *Uvigerina spinicostata* Cushman and Jarvis, 1929, var. ERRATA *nom. nov.* for (in accordance with Art. 25, c-2 of the Internat. Rules of Zool. Nomenclature): *Uvigerina spinicostata* Cushman and Jarvis, 1929, var. *alazanensis* Nuttall, 1932, (non *Uvigerina alazanensis* Nuttall, 1932), Jour. Paleontology, vol. 6, p. 23, pl. 6, fig. 1; and for: *Uvigerina spinicostata* Cushman and Jarvis, 1929, var. *acuminata* Thalmann, 1939 (non *Uvigerina acuminata* Hosius, 1893), Paläont. Zeitschr. vol. 13, p. 340, lower Oligocene, Mexico.

Listerella (now *Schenckiella*) *laevis* Cushman, 1940, Cushman Lab. Foram. Research. Contr., vol. 16, p. 54, pl. 9, fig. 8, from the Paleocene of Alabama is preoccupied by *Listerella levis* Finlay, 1939, Trans. Roy. Soc. New Zealand, vol. 69, p. 97, pl. 14, fig. 79 from the Middle Eocene of New Zealand.

Planulina palmerae Garrett, 1942, Jour. Paleontology, vol. 16, pl. 70, figs. 3, 4, from the Miocene of Texas, is preoccupied by van Bellen, 1941, Proc. Nederl. Akad. Wetensch., vol. 44, p. 1144, figs. 7–9 from the Lower Oligocene of Cuba.

Cibicides subtenuissimus (Nuttall, 1928) var. *concava* F. G. Keijzer, 1945, Proefschr, (Thesis) Univ. Utrecht. p. 208, pl. 4, fig. 61 from the Oligo-Miocene of Cuba, is preoccupied by Tolmachoff, 1934, Ann. Carnegie Mus., vol. 23, p. 339, pl. 42, figs. 22–24 from the Miocene of Colombia. *Cibicides concavus* Dorn (MS) in LeRoy, 1941, Quart, Colorado School of Mines, vol. 36, p. 47, pl. 2, figs. 82–84 from the Mio-Pliocene of Borneo is, therefore, also preoccupied by Tolmachoff, 1934, and should be renamed by its author. All homonymists, J. A. Cushman, J. B. Garrett, Jr., and F. G. Keijzer have duly been informed by letter with regard to their respective homonyms in accordance with the "Code of Ethics" attached to Art. 34 of the Internat. Rules of Zool. Nomenclature as stipulated by the Monaco-Congress in 1913. Authors of homonyms in Foraminifera, who have been duly informed either by letters or by publication of periodical lists of foraminiferal homonyms, and who have not yet offered substitution-names, are urgently requested to read carefully pp. 191 and 192 of Rud. Richter's excellent "Einführung in die Zoologische Nomenklatur durch Erläuterung der Internationalen Regeln," 2nd edition, Frankfurt am Main, 1948 (Senckenberg-Buch 15).

JOURNAL OF PALEONTOLOGY, VOL. 23, NO. 5, PP. 507–509, PL. 82, SEPTEMBER 1949

THREE NEW DEVONIAN SPECIES OF *MICROCYCLUS* FROM MICHIGAN AND ONTARIO

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ABSTRACT—Three new species of *Microcyclus* are described and illustrated. One is from the Arkona shale and the second from the Hungry Hollow formation, both Middle Devonian of the Thedford region, Ontario. The third is from the Middle Devonian Alpena limestone of the Traverse group, Alpena, Michigan. Hypotypes of *Microcyclus discus* Meek and Worthen, the genotype species, and of *M. thedfordensis* Bassler are illustrated.

INTRODUCTION

AN excellent revision of the known genera and species of the Paleozoic discoid and cushion-shaped Tetracoralla without tabulae or dissepiments was given by Bassler (1937, pp. 189–201). Hill (1936, pp. 189–217) has shown that the Silurian forms in this group are characterized by radially arranged acanthine septa with no modification of the protosepta, while the Devonian and Carboniferous forms have lamellar septa arranged in quadrants with the protosepta modified to form one or more fossulae. The differences between the Silurian and post-Silurian forms are considered to be of sufficient magnitude so that a new family name is proposed for the latter in the writer's recent memoir of the Geological Society of America on the revision of the families and genera of the Devonian Tetracoralla.

Three new species of *Microcyclus*, a characteristic Devonian genus, have been recognized in the University of Michigan collections. The first two species, *Microcyclus bifidus* and *M. erraticus* are from the Hamilton group of the Thedford region, Ontario, where *M. thedfordensis* Bassler is the common species. *M. bifidus* and *M. thedfordensis* are from the Arkona shale, while *M. erraticus* is from the overlying Hungry Hollow formation and is the first species of the genus to be reported from this formation. The third species, *M. alpenensis* is from the Alpena limestone at Alpena Michigan, and is the first record of the genus in the Traverse group.

DESCRIPTION OF SPECIES

GENUS MICROCYCLUS Meek and Worthen

Microcyclus, MEEK and WORTHEN (1868, p. 420).

Genotype.—By monotypy, *Microcyclus discus* Meek and Worthen (1868, p. 420, pl. 11, figs. 7 a–b).

Generic description (Bassler, 1937, pp. 193–194).

Thin, discoidal, almost flat free coralla with a small central irregular basal scar of attachment and a shallow calyx provided with smooth septa arranged in four groups separated by fossulae of which the cardinal one, with a conspicuous cardinal septum, is best developed. Major septa merging into a smooth central area; minor septa short and often attached to the major. The smooth septa and conspicuous cardinal fossula with its cardinal septum are characteristic of *Microcyclus*, which represents the stage of development in the family at which all the fossulae but the cardinal one are inconspicuous.

MICROCYCLUS BIFIDUS Stumm, n. sp.
Plate 82, figures 8–10

Description.—Coralla thin, discoid, ranging from 10 to 14 mm. in diameter and averaging 2 mm. thick. Proximal side provided with a concentrically banded epitheca showing an attachment scar in the axial region. Distal surface with 40–48 bifid septa, each with a distinct medial groove. Major septa extend from periphery about two-thirds the distance to the axis, merging into a smooth, relatively horizontal axial area. Minor septa about one-third as long, free at their axial ends. Cardinal fossula indistinct, produced by depression of distal surface.

Remarks.—This species approaches the size of *M. discus*, the genotype species (see pl. 82, figs. 1–3), but is easily distinguished from it by the presence of bifid septa and by the fact that the minor septa are free at their axial ends, while in *M. discus* they are attached to neighboring major septa. The bifid septa and the less well defined cardinal fossula distinguish *M. bifidus* from its stratigraphic associate *M. thedfordensis* Bassler (see pl. 82, figs. 11–14). The latter species is quite variable with regard to length of major septa and development of cardinal fossula.

Occurrence.—Middle Devonian, Hamilton group, Arkona shale; Thedford region, Ontario, Canada.

Types.—Holotype no. 25752; paratype no. 25753, Museum of Paleontology, University of Michigan.

MICROCYCLUS ERRATICUS Stumm, n. sp.
Plate 82, figures 4–6

Description.—Corallum discoid, very thin, ranging from 10 to 12 mm. in diameter and from 1 to 2 mm. thick. Proximal side with thin, concentrically banded epitheca through which the proximal edges of the septa are faintly visible. Central attachment scar present. Distal surface with about 40 septa of which the major, moderately thick near the periphery, become attenuate and irregularly twisted in their axial parts. In some of the septa the twisting is so extreme that they reverse direction and extend toward the periphery a short distance at their axial ends. Minor septa about one-third as long as major, some free, others attached to neighboring major septa at their axial ends. Fossula indicated by a depression along one side of corallum.

Remarks.—The peculiar twisting habit of the major septa serves to distinguish this species from all other known forms of *Microcyclus*.

Occurrence.—Middle Devonian, Hamilton group, Hungry Hollow formation, coral bed; Hungry Hollow, 2 miles north and ¾ mile east of Arkona, Ontario.

Type.—Holotype, no. 25720, Museum of Paleontology, University of Michigan.

MICROCYCLUS ALPENENSIS Stumm, n. sp.
Plate 82, figure 7

Description.—Corallum thin, discoid, averaging 11 mm. in diameter and ranging from 1 to 2 mm. thick. Proximal side with concentrically banded epitheca. Distal sur-

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EXPLANATION OF PLATE 82

All figures are ×2.

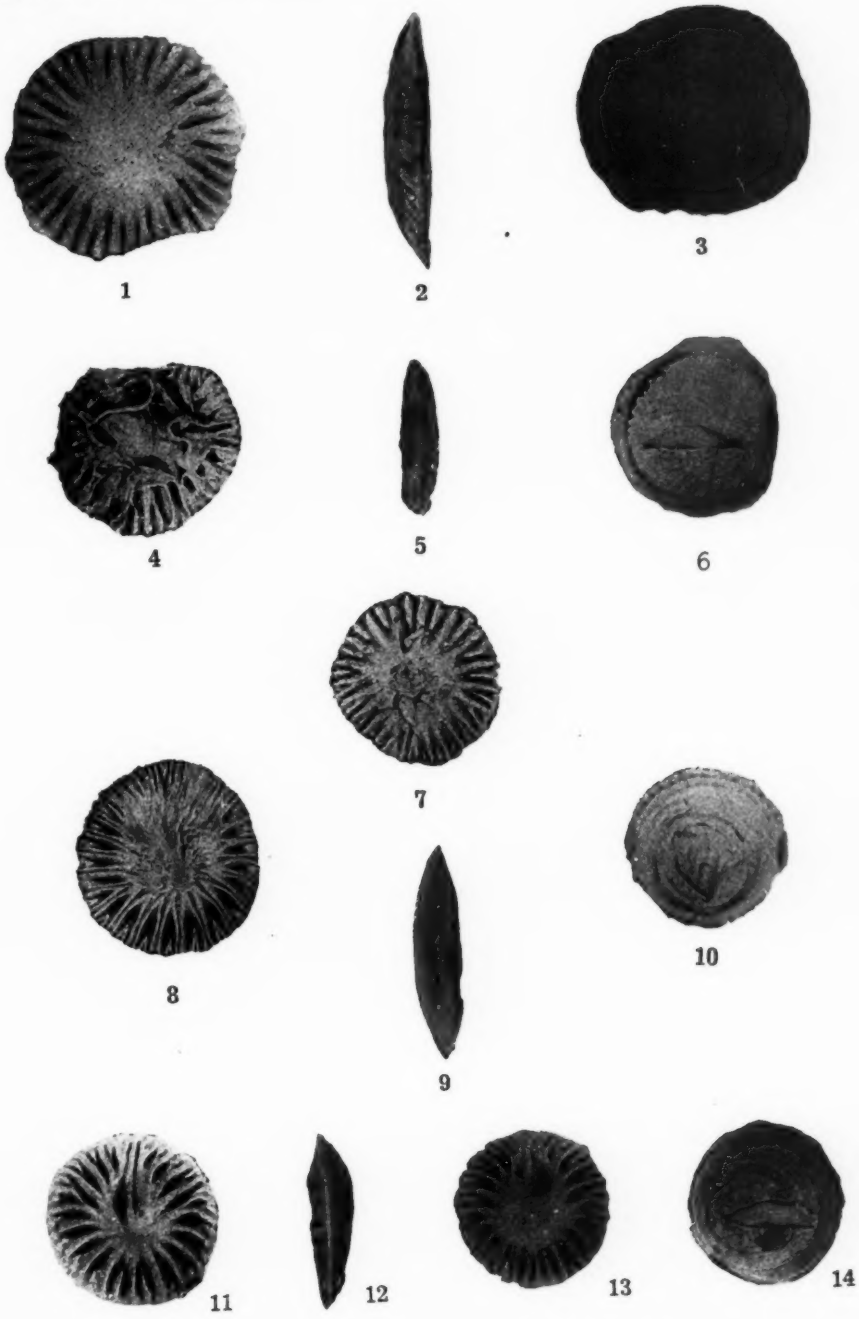
FIGS. *1–3*—*Microcyclus discus* Meek and Worthen. *1*, Distal view of hypotype no. 23149 Museum of Paleontology, University of Michigan, showing minor septa attached to major at their axial ends. Middle Devonian, St. Laurent limestone, "Devil's Back-bone," Grand Tower, Illinois. *2*, Side view of same specimen showing convexity of axial region. *3*, Proximal view of same specimen showing concentrically banded epitheca. (p. 507)

4–6—*Microcyclus erraticus* Stumm, n. sp. *4*, Distal view of holotype, no. 25720 Museum of Paleontology, University of Michigan, showing irregularly twisted major septa. *5*, side view of same specimen. *6*, Proximal view of same specimen showing thin epitheca and septal ridges. (p. 508)

7—*Microcyclus alpenensis* Stumm, n. sp. Distal view of holotype, no. 25719 Museum of Paleontology, University of Michigan, showing short, alternating septa and smooth, depressed axial area. (p. 508)

8–10—*Microcyclus bifidus* Stumm, n. sp. *8*, Distal view of holotype, no. 25752, Museum of Paleontology, University of Michigan, showing bifid septa. *9*, Side view of same specimen. *10*, Proximal view of paratype, no. 25753, Museum of Paleontology, University of Michigan showing epitheca and attachment scar. Both specimens from Middle Devonian, Arkona shale, Thedford region, Ontario. (p. 507)

11–14—*Microcyclus thedfordensis* Bassler. *11*, Distal view of hypotype, no. 25755, Museum of Paleontology, University of Michigan, a specimen with long major septa and a well developed fossula. *12*, Side view of same specimen. *13*, Distal view of hypotype, no. 25754, Museum of Paleontology, University of Michigan, a specimen with short major septa, wide axial area, and relatively obscure fossula. *14*, Proximal view of same specimen. Both specimens from Middle Devonian, Arkona shale; Hungry Hollow, 2 miles north and ¾ mile east of Arkona, Ontario. (p. 507)



Stumm, Middle Devonian *Microcyclus*

face with about 44 short, relatively thick septa of which the major extend from one-half to two-thirds the distance to the axis, leaving a smooth, depressed axial area. Minor septa about one-half as long as major, free at their axial ends. Cardinal fossula very indistinct, produced by slight depression on one side of corallum.

Remarks.—This species is similar to *M. discus* in general appearance but is smaller in all proportions. In addition the minor septa of *M. discus* are attached to the neighboring major septa at their axial ends while in *M. alpenensis* they are free.

Occurrence.—Middle Devonian, Traverse group, Alpena limestone, *Longispina emmetensis* zone, one-foot shale bed 50 feet below top of formation, Alpena, Michigan.

MANUSCRIPT RECEIVED JANUARY 13, 1949.

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JOURNAL OF PALEONTOLOGY, VOL. 23, NO. 5, PP. 510–514, PL. 83, SEPTEMBER 1949

FACIAL SUTURES IN THE (HYPOPARIAN) TRILOBITES *LOGANOPELTOIDES* AND *LOGANOPELTIS*, AND THE VALIDITY OF THESE GENERA

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ABSTRACT—*Loganopeltoides*, erected by Rasetti in 1945, was distinguished from *Loganopeltis* (Rasetti 1943) on the ground that it had a dorsal facial suture, which could be either the anterior branch in an opisthoparian, or the anterior coincident with the posterior branch in a proparian trilobite. But later the same genus was interpreted by him as exhibiting the two branches of the facial suture of an opisthoparian.

The writer believes, on the contrary, that no facial sutures exist at all, and that these genera are one and the same. He shows that the genus is a close relative of *Harpides*, and briefly discusses its relationships.

THE present paper was substantially written in the winter of 1945–6 in response to that by Rasetti in the Am. Jour. Sci. 1945 entitled "Evolution of the Facial Sutures in the Trilobites *Loganopeltoides* and *Loganopeltis*." It was offered for publication, and was submitted to Professor Rasetti; but it was not published at once, because Rasetti had more to say upon the subject. This has been published in this Journal (1948, pp. 25–29), but in the writer's view he has not proved his claim, and criticism is still desirable. Also the rare relatives of these trilobites have a rather special interest.

Our knowledge of Cambrian and Ordovician trilobites has been increasing very rapidly thanks to the work of Rasetti; and it is among those from the pebbles of the Levis conglomerate of early Ordovician age in Quebec that those here reviewed mainly occur.

The genus *Loganopeltis* was erected by him (1943, p. 103, Pl. 19) for his *L. depressa* and for '*Conocephalites*' *zenkeri* Billings. He referred his own species associated with *Pilekia eryx* to the Lower Ordovician, and Billings' to the Upper Cambrian (pp. 101, 104); but both may be found to be above the *Dictyonema* shale.

Billings had only a cephalon for his '*Conocephalites*' *zenkeri*, which he describes in detail without mentioning facial sutures (1865, p. 398, fig. 375). But since he does not mention sutures in any of the trilobites which he referred to this genus, and since he compared one of them, his '*Conocephalites*' *adamsii* (loc. cit. p. 13) with Barrande's '*C.*' *sulzeri* and '*C.*' *coronatus*, now genotypes respectively of *Conocoryphe* and *Ctenocephalus* in the Conocoryphidae, he implied that facial sutures were absent; for where facial sutures were present he defines them. The head of '*C.*' *zenkeri* he describes as very convex; and his fig. 375 exhibits cracks from both right and left eyes out to the nearest points of the margin. The cracks are not quite straight, and the two are not symmetrical. They can be regarded as the effects of gravity within the sediment upon a convex head strengthened up to the eye 'holes' by the glabella and the ocular ridges. One can be confident that Billings regarded these lines as cracks.

Rasetti's own species *L. depressa* (1943, figs. 1–3; 1945, figs. 4–7) has a slightly wider brim, which is distinct also in its sculpture and is without cracks or sutures. He compared it with *Harpes* and *Entomaspis;* but states that "the structure of the pygidium is altogether different from that found in *Harpes*, *Entomaspis*, and most hypoparian trilobites." For *Entomaspis* see Ulrich 1930.

But his material comprised the greater part of the thorax (17 segments visible) as well as the pygidium. Indeed, except for the hypostome and the doublure with probable genal spines, it is fairly complete. The head and thorax, however, prove conclusively

that these are related to—are indeed the most primitive forms yet known—of the remarkable and rare genus *Harpides* Beyrich; and the pygidium furnishes knowledge of this member for the first time.

Curiously, Billings himself (loc. cit. p. 333) identified an isolated imperfect glabella as "*Harpides ? desertus* n. sp."; and this is apparently indistinguishable from the glabella of *Loganopeltis zenkeri* (Billings). He also described a glabella and brim as *Harpides atlanticus* Billings, and another brim as *H. concentricus* Billings (loc. cit., pp. 281, 282), from beds containing typical Lower Ordovician graptolites and trilobites. Both these *Harpides* fragments are specifically distinct from the forms above mentioned and are more specialised. Billings (p. 282) states that *H. atlanticus*—"must be very closely allied to *H. rugosus*" (Sars and Boeck), "which occurs in Norway and Sweden" (Angelin 1854, Tabl. 41, fig. 7). Angelin's figure was supplemented by two papers in the same year: Moberg and Segerberg supplied the occipital ring (M. and S. 1906, p. 85 and Tafl. 5, fig. 1); and Post figured again Angelin's fragmentary type specimen, besides a new complete head shield a little larger, and the central part of one much bigger (Post 1906, p. 476; figs. 3–5); see our figs. 1 and 2, Pl. 83. The complete cephalon is much broader than is represented by Angelin, and this, combined with the correction of the eye-lines and eyes, strongly suggests the identity of this Scandinavian species with the form later described by Barrande under the name *Harpides grimmi* (1852, p. 931), and described again and also figured in the Supplement (1872, p. 22, Pl. 1, figs. 11–14) reproduced in our figs. 3–6; which will probably therefore have to be called *H. rugosus*. In this, as in *H. atlanticus* Bill., the brim where narrowest in front of the glabella is about twice as wide as the length of the glabella, and is traversed from the glabella out by a relatively coarse radial network of nervures. This unique fossil described by Barrande had apparently been quite complete, with rostrum and hypostome. It is a large trilobite 7.6 cm. wide, and the complete animal cannot have been less than 11 cm. long: its form seems adapted for enrolment, the pleurae having rounded ends. The thorax adjoins the head, but the specimen was broken away behind, leaving evidence of 21 thoracic segments. The surface exhibited follows the hypostome (instead of the surface of the glabella), and it follows also the wide doublure round the head and thorax (instead of the dorsal test) so that we do not know the outer brim, and hence, to what extent the pattern of nervures changes over this latter. Judging however from the figures of the Scandinavian specimens above mentioned this is probably slight, till the narrow rim is reached. It is perhaps the only specimen which hitherto has shown the doublure. This is of an even width of more than 1/3 the length of the cephalon and is traversed, from one genal angle to the other by two ventrally directed ridges, defining approximately the median 1/5 of its width. These ridges may perhaps represent the 'girder' in *Trinucleus*. The doublure is without pits or radial sculpture, and thus is very different from that of *Harpes* with its system of pits opposing those of the dorsal test. Judging from Barrande's figure, '*H. grimmi*' was provided with narrow genal spines which turn outward from the line of the lateral margin. This outward bend is very marked also in *Harpides villebruni* (Bergeron), in which however the genal spine issues from opposite the midlength of the shield (Bergeron 1895, p. 29, Pl. 4). The doublure is missing in Rasetti's material of *Loganopeltis*, and he thought that genal spines are—"absent, unless they are borne by the epistomal plate, which is unknown" (1945, p. 46). But in view of their presence in *Harpides* and in *Entomaspis*, in each case borne by the ventral plate, and from the fact that one would not suspect their existence even in trinucleids if we had no ventral plate, one can fairly confidently believe that genal spines were borne by the doublure. To this Rasetti agrees in his 1948 paper, p. 29.

The thoracic pleurae in '*Harpides grimmi*' are of the same shape as those of *Loganopeltis depressa* Rasetti, which however fail to show their ends. The tips in '*H. grimmi*' are rounded in contrast with those of *H. hospes* Beyrich (see Barrande 1852, p. 5, fig. 3a) and *H. villebruni* (Bergeron).

The pygidium of *Loganopeltis depressa* (1943, fig. 3; 1945, fig. 7) and of *L. zenkeri* (1944, p. 238, fig. 47) is longer than wide,

with a short rachis exhibiting a few rings (3) and then tapering into a median rib, and with four bold pleural ribs on each side alternating with fine ones curving abruptly round to the rear, the outer ones to well beyond the tapering rachis, to end in broad points, between which is a rather angular, median embayment. The primitive characteristics of this tail are of interest. Its bold and fine alternating ribs correspond to the broad and narrow ribs of the thoracic pleurae: it is as if these backwardly directed pleurae had only just joined up into a pygidium. This pygidium enables us to postulate for the first time a member of like character for '*Harpides grimmi*,' but the ends of the pleurae are in this rounded, as if for enrolment; and hence its margin we can suppose to have been even. Above are mentioned all the species of *Harpides* known to the writer, except for the very fragmentary *H. plautini* Schmidt (Schmidt, 1894, p. 63; Pl. 5, figs. 1 and 2), and a beautiful *Harpides* perhaps blind, specialised quite differently from *H. rugosus*, which Rasetti has discovered in Lower Ordovician boulders at Levis, and of which he has not yet published a description.

In his 1944 paper Rasetti discusses the facial sutures of these forms: he acknowledges that—"in *L. depressa* there is no trace of dorsal sutures"— but—"in *L. zenkeri* all specimens show something like a ridge, which starts from the eye and is directed outward and forward reaching the margin of the cephalon"—which—"suggests the anterior branch of the facial suture." But after much discussion he "refrains from expressing a final opinion."

In his paper of 1945 on this subject he briefly discusses to some extent the facial sutures of trilobites in general and the origin of the hypoparian forms. With regard to *Loganopeltis* he concludes—"that the only dorsal suture existing in *L. zenkeri* is a suture running forward and outward from the eye to the margin of the cephalon." Previously it had—"appeared possible that *L. zenkeri* was a proparian trilobite possessing a narrow libragene limited by two (close) parallel sutures. The examination of better preserved material clearly indicates the existence of only one suture."

At the same time a small cephalon accompanying *L. zenkeri* is referred to the new species *L. minutus* Rasetti; but both the cephalon and pygidium of this form can be attributed to *L. zenkeri*, for greater differences than these exhibit occur within a species (cf. 1944, Pl. 38, fig. 26 with 1945 Pl. 1, fig. 3; and 1945, fig. 1 with fig. 2). But for the present discussion the interest of the little cephalon is that it also exhibits these cracks across the shield. Because of these supposed sutures a new genus '*Loganopeltoides*' is instituted for them, and they are supposed to have given rise to *Loganopeltis*.

But Rasetti has already remarked the—"unusually thin test of the trilobite"—and in the total absence of dorsal facial sutures the test (already dismembered, for all have lost the doublure) has broken just where it was weakest—between the "eye-hole" and the nearest point of the margin. The same error of mistaking cracks for facial sutures has been often made before. In the Olenellidae, for example, there are no open facial sutures, and the test is both convex and excessively thin (Raw 1931): the visual surface of the eye is seldom preserved, being represented usually by a hole through the test; and the cephalon frequently breaks between the eye and the nearest part of the semicircular margin, and also between the posterior end of the eye and the posterior margin; and cracks in one or both of these directions have been mistaken for sutures by Whitfield, Walcott, Raymond and Bell (Raw 1925, pp. 301–305 and Raw 1937, p. 300). If one takes Walcott's 1910 mono-

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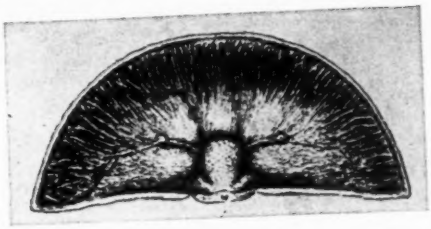
EXPLANATION OF PLATE 83

FIGS. *1*, *2*—*Harpides rugosus* (Sars and Boeck from Orreholmen, Sweden; both copied from Post, 1906, Tafl. 13; slightly enlarged (×20/19).

3–6—"*Harpides grimmi*" Barrande from shales of de Maria Vermahulung iron mine, Katschina, southeast of Rokitzan, Bohemia; all copied from Barrande 1872, Pl. 1, and showing the extent of the cephalic and thoracic doublure. *3*, *4* and *5* ×1. *4*, median longitudinal profile. *5*, profile of a thoracic segment. *6*, part of a thoracic segment; ×2.

1



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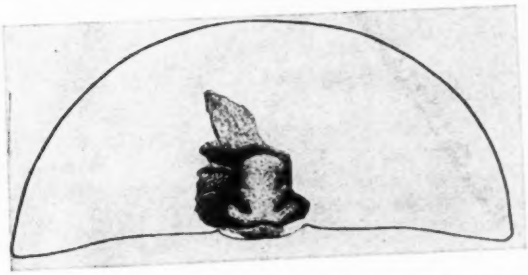

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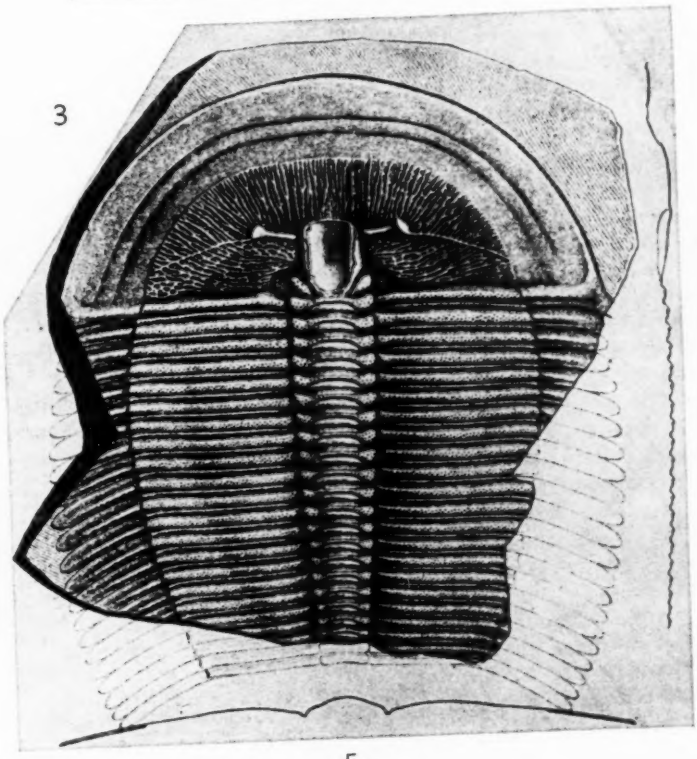

4

5

6

Raw, Trilobite facial sutures

graph or the latest work in which Olenellidae extensively figure, one can see by scanning the figures how frequent are the fractures in these directions (Resser and Howell 1938).

In his discussion Rasetti offers two possible origins of the supposed anterior 'sutures': either—"(1) '*Loganopeltoides*' derives from an opisthoparian trilobite, and the posterior branch is in a state of symphysis;"—or—"(2) it derives from a proparian, and the two branches of the facial suture became closer and closer to each other until the libragene completely disappeared, the two sutures becoming one."

In the latest presentation of his views (1948) he describes again *L. zenkeri* and *L. minutus* with their supposed sutures; and illustrates them again by enlarged photographs. The first named species is claimed to show the sutures in coincidence, the second to show two sutures which run parallel within a very short distance from one another. The writer has examined all these, and thanks to Rasetti's kindness has examined direct photographs and a beautiful cast, but he is quite unconvinced that they are other than cracks of these thin tests, which had all apparently been dismembered before entombment, having all lost their doublures. The 'two sutures' of *L. minutus* are apparently simply a single opened crack. Rasetti tries further to fortify his claim by describing a new species *L. kindlei* from Newfoundland; but the writer quite fails to see anything but cracks and the breaking away of the eyes in exposing the fossil, as obtains also in the other specimens; and till better evidence is advanced, the matter must for him be left in doubt.

Rasetti at the same time modifies his previously expressed view as to the origin of the hypoparian condition: now (l.c. pp. 27 and 28) he considers that it derives from an *opisthoparian* such as *Cedaria* (Walcott, 1925, p. 79, Pl. 17, figs. 18 to 24), the branches of the facial suture of which came together; coalesced into one, forming a ridge; they then disappeared, and we have a hypoparian trilobite like *Trinucleus*. One cannot say that it was never as he imagines, but probably many will fail to see that *Loganopeltoides* tells us anything about it. There are very good reasons to believe that no such coalescence of the branches of the sutures preceded the condition which we get in the Olenellidae, the Conocoryphidae and the Trinucleidae. The Harpedidae have perhaps no known near relations that are not hypoparian; but in the Trinucleidae we have *Orometopus*, which certainly does not support the view that the branches of the suture coalesced; for though already a trinucleid, it has still reduced compound eyes and facial sutures, the branches of the latter making a right angle with one another (Raw in Lake, 1907, pp. 46 and 47, Pl. 4, figs. 6–9).

The Lower Cambrian Olenellidae display the vestiges of their dorsal facial sutures, and these suggest the origin of their metaparial head plan, marginal suture and crescentic rostrum (Raw, 1925, pp. 301–305; 1936, pp. 245–247, figs. 4, 7, 8a, 8b; 1937, pp. 531–587). But had we been limited to Ordovician descendants, probably no vestiges of the dorsal facial sutures would have survived; and we should have been faced with a problem such as the Harpedidae present. If Middle or Lower Cambrian representatives of the family are ever found, it may then be easy to solve their problems. Till then let us not speculate too wildly.

If the contention, that the supposed sutures of "*Loganopeltoides*" are cracks, is sustained; and Rasetti has not satisfactorily proved his case; then this genus is invalid and the species revert to *Loganopeltis*. This latter with the earlier generic name stands however on a quite different footing: it denotes a form very closely related to *Harpides;* but now that genera are so restricted, both are valid genera. *Harpides* is much the more specialised in its cephalon. The glabella is much abbreviated; and, to judge from *Harpides rugosus, Harpides hospes* and Rasetti's new species, the glabellar furrows are almost reduced to the posterior pair, whereas in *Loganopeltis* (Rasetti, 1945, Pl. 1) the glabella is but little reduced beyond the conical form characteristic of, say, the Middle Cambrian Ptychoparidae: only the frontal lobe is much reduced and all the usual three pairs of glabella furrows are well retained as they not infrequently are in *Harpes* (*Eoharpes*). The brim again in *Harpides* is on an altogether larger scale, making the length of the head three times as long as the glabella and its width six times as wide, whereas in *Loganopeltis* the same

measures are less than twice and four times respectively.

These genera seem to be related to Trinucleidae as well as to Harpedidae, and should constitute a new subfamily of the latter, which would be most appropriately named Harpidinae. Their distribution is of interest: *Loganopeltis zenkeri* is a constituent of the *Hungaia magnifica* fauna attributed to the Cambrian; the others are Ordovician—*L. depressa* is "early Canadian," the European *Harpides* are all members of the '*Ceratopyge* fauna' which follows that of the *Dictyonema* shale. Regarding the *Hungaia magnifica* fauna Rasetti has done a great service by presenting them magnificently in numerous photographs (Rasetti 1944); but not a single form can be recognised as common also to Europe. *Hungaia* itself, e.g. *H. quadrisspinosa* Rasetti presents perhaps as close comparison as any. It appears to be a near relation of *Dicellocephalina dicraeura* Ang. (Moberg and Segerberg 1906, Tafl. 5) and *D. furca* Salter (Lake 1919, p. 118, Pl. 14), which are more primitive in the glabella and more advanced in the pygidium. Perhaps there is little difference of geological age between them. In Europe it is an immigrant fauna bringing in the first Trinucleidae and Raphiophoridae, as well as *Eoharpes* and *Harpides* besides several other families. Asaphidae however had entered a little earlier.

Finally I should like to thank Rasetti for the interest of his papers, which have furnished the subject for this communication.

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JOURNAL OF PALEONTOLOGY, VOL. 23, NO. 5, PP. 515–517, PL. 84, SEPTEMBER 1949

TRIASSIC CHIMAEROID EGG CAPSULES FROM THE CONNECTICUT VALLEY

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ABSTRACT—To the recently described chimaeroid egg capsules a new species *Chimaerotheca oakesi* is added, and its relation to the shark-like fish *Carinacanthus jepseni* Bryant is discussed. The ecological and physiographic conditions of some parts of the Eastern Triassic basin are briefly mentioned.

INTRODUCTION

TO THE rare finds of egg capsules of chimaeroid fishes reported by Brown (1946 and Warren (1948) we can now add a number of smaller egg cases, doubtless belonging to a related type, from Upper Triassic gray shales in the Connecticut Valley near Turners Falls, Massachusetts. Mr. Frederick Oakes, principal of a local school, gave the fossil to the writer for identification during the latter's investigation of the Triassic deposits in that neighborhood. It had been looked upon as a crustacean fossil similar to small phyllopods of the Newark series, suggesting some affinity with that group, as was suspected in the case of the German species before it was identified as an egg case. However, Brown's references and Warren's description of a Cretaceous chimaeroid egg capsule from Canada clearly demonstrate that these fossils from the Triassic at Turners Falls belong to the same genus.

CHIMAEROTHECA OAKESI, Bock, n. sp.
Plate 84, Figures 1–3

Several specimens are represented on both sides of a small piece of gray-blue shale about 1 cm. thick. Three of them are more or less complete, while others are fragmentary. In all there are about a dozen specimens. The original substance of the egg capsules is replaced by a hematitic, rather coarse, material, showing some of the rugae as gray outlines. Specimen no. 1 displays the dorsal side, while no. 2 and 3 show the ventral surface. The shape of the egg case is cordate, 3 cm. long and 2.5 cm. wide. There appears to be a caudal appendage 1.5 cm. long and 2 mm. wide, which often is separated or in a displaced position.

The embryo case proper is well centered, cylindrically shaped, and tapered at both ends. It is 1.5 cm. long, 3 mm. wide, and 2 mm. thick. The dorsal side seems to be slightly keeled. It is divided into about 15 to 20, mostly indistinct, segments having on each side, where the ribs or rugae seem to be attached, a dot-like projection. The posterior end of the embryo case terminates in the appendage, which appears to be rather solid. It is not embraced by the web or rugae as in similar species cited by Brown.

The web, or lateral membrane, is marked on its ventral surface by 25 to 28 leg-like curved rugae bent at the anterior portion in a forward direction, and it is terminated by two strong, sinuous arm-like appendages, which extend about 5 mm. above the anterior portion of the embryo case. In the middle section the rugae are oblique to the case. At the posterior end they bend gradually backward in the direction of the caudal portion. The lateral part of the rugae, particularly at the anterior end, is irregularly branched and slightly sectional. The surface of the ventral side of the web is covered by a brownish, shiny, somewhat transparent, apparently chitinous substance.

The dorsal surface of the egg case (figure 1) has a wing, or shell-like, appearance and is covered with fine striae parallel to the median axis of the embryo case. The rugae do not penetrate this surface, save for the lateral anterior and posterior portions, where they partially cut through the membrane surface. The over-all thickness of the web, including the rugae, is about 0.8 mm.

Discussion.—While there exists a general similarity of this species to *Chimaerotheca newmexicana* Brown and *Chimaerotheca*

stelcki Warren, there are also some marked differences in shape, dimensions, and structural details, which suggest that it is distinct from these species. The segmented embryo case is not apparent in any of the fossil egg capsules, but is faintly visible in the case of the living *Harriotta* species shown by Brown. (1946, pl. 39, fig. 7.) Otherwise, this new species appears to be referable to Brown's form genus *Chimaerotheca*. There is no doubt that our new species is the smallest form of a chimaeroid egg case so far known. Applying Dean's suggestion (1906, p. 134) that the adult fish is about four times the size of its egg case, the fish, which produced this new species of egg capsule, must have been 16 to 18 cm. long. Many of the Triassic waters in the Newark basin were crowded with numerous species of fish of different sizes. *Diplurus longicaudatus* Newberry, a large coelacanth, reached 80 cm. in length, while most of the remaining Triassic fish species, such as the common ganoids, *Semionotus* and *Redfieldia*, are of a size comparable to the fish which was responsible for *Chimaerotheca oakesi*.

There is no indication that any of the known Triassic fishes reproduced by egg cases. Only the living classes, such as sharks, rays and chimaeroids, shelter their eggs in capsules, though some of the sharks are also ovoviviparous. Several of the rays and sharks produce egg cases which are quite similar, rectangular, cushion-like, forms, with long tendrils from each corner, a quite different design from that of the chimaeroids. It is, therefore, astonishing that the latter should have been as frequent in an environment which was inhabited by quite a dissimilar group of fishes. However, there is one exception. W. L. Bryant (1934) described from the fish beds of the well known Gwynedd tunnel deposits in the Lockatong formation of the Pennsylvania Triassic a shark-like fish, *Carinacanthus jepseni*. The same deposits have yielded many fossils, including numerous fish species and reptilian remains, among them the bones of the tiny *Gwyneddosaurus*. (Bock, 1945).

The shark-like creature, *Carinacanthus*, was unfortunately found without a head, but is of unusual interest from an evolutionary and ecological view point. Though the cartilaginous chimaeroids and selachii are not closely related, they possess some identical features which makes their distinction in poorly preserved fossils quite difficult. Both classes may have an anterior dorsal fin with a distinct, sharp spine. In the sharks, the main spine and the consecutive ones are attached to individual bases, while the spines of the chimaeroids are based on a single undivided radial cartilage plate. The base of the anterior spine in Bryant's species is not clearly defined. But his fish also shows a spine at the posterior dorsal fin, which is absent in the chimaeroids This feature should be sufficient to establish the selachian origin of *Carinacanthus*. However, Bryant also points out (p. 322) that "the comparatively large second dorsal fin spine is an unusual feature," and as it does not appear to be physically connected, it may be possible, that it is a displaced one, which might suggest relationship of his fossil to a chimaeroid fish.

The European Triassic shows ample evidence of a selachian fauna, though it seldom produces more than teeth and spines. Only one of the genera, *Nemacanthus* Agassiz, has been assigned by Alberti (1864) to the Chimaeridae, which identification also was verified by later investigations by E. v. Stromer. *Nemacanthus monilifer* Agassiz, from the Rhaetic bone beds of Swabia, has a striated spine, similar in shape and size to that of *Carinacanthus jepseni* Bryant, but conclusive comparative material is missing. Whatever kind of relationship may exist between the supposed Gwynedd shark and the chimaeroid egg capsules from the Triassic of the Connecticut Valley, these two new species represent an important and interesting development of the so far known Triassic fish fauna of the Newark series.

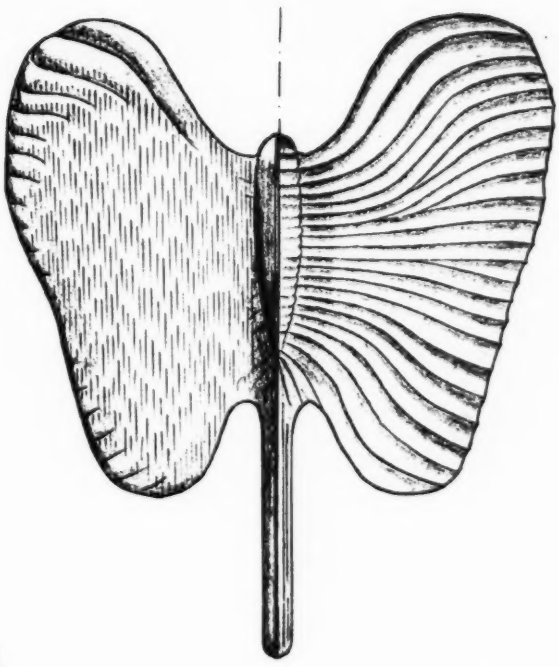
Some ecological observations seem to the writer to be worth discussion. It has already been mentioned that there exists a pro-

EXPLANATION OF PLATE 84

FIGS. *1–3*—*Chimaerotheca oakesi* Bock, n. sp., all ×2. *1*, a dorsal view; *2*, an interior view; *3*, a diagrammatic composite view, of which the left half is an external dorsal view and the right half an inner view (with the external cover removed).

1

2



3

Bock, Triassic chimaeroid egg-cases

nounced resemblance of some of the chimaeroid egg cases to some crustaceans. As the survival of the whole species depends on these cases, which are helplessly attached to some objects of their aquatic environment, exposed to predators, the appearance of a crustacean-like, horny, unattractive, lifeless object seems to indicate a mimicry, or a protective design, to discourage any interest of carnivores in these egg cases. Coprolites indicate that contemporaneous small phyllopods, (Pseudoestheriae), formed an important link in the food chain of the Triassic waters, though they were sheltered in a bivalved shell. It would seem that much more attractive chimaeroid embryos needed a corresponding, or better, protection, which appears to be met by the development of the peculiar ribbed design of the comparatively large membrane.

Another problem of environment is presented by the appearance of chimaeroids in the Newark basin. While certain species of living sharks flourish in the fresh water of lakes and estuaries, the chimaeroid fishes are limited to a marine habitat. The evidence so far discovered points to fresh water conditions throughout the eastern North American Triassic. Fresh water algae and a predominating continental fish fauna, particularly the genus *Semionotus*, which is known from the Triassic beds of Nova Scotia, the Connecticut Valley, and more southern areas, indicate that there existed for shorter or longer periods a drainage, probably through the entire chain of eastern Triassic troughs, in a northern direction, which is shown by water flow marks. An estuary to the north does not seem unlikely from present indications, and such a seaward outlet would explain the occasional appearance of marine forms in the Newark rocks. Temporary inundations by the sea, such as are indicated in sections of the Upper Triassic in central Europe, which left unmistakable evidence (the bivalve *Avicula*) are so far unknown in the Newark basin, and its fresh-water origin can not be seriously disputed.

Types.—The holotype (1) and the paratypes (2 and others) are deposited as no. 20002 in the Bock collection, Academy of Natural Sciences, Philadelphia.

Occurrence.—Upper Triassic of Massachusetts. From bluish gray well-laminated fresh-water shales near Turners Falls at Hale's farm. The locality is also known for its abundance of dinosaur tracks, conifers, and algae.

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JOURNAL OF PALEONTOLOGY, VOL. 23, NO. 5, PP. 518–520, SEPTEMBER 1949

THE RELATIONSHIPS OF THE ALBERTA CRETACEOUS DINOSAUR "*LAOSAURUS*" *MINIMUS* GILMORE

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ABSTRACT—The hind foot and portions of the limb of a small ornithopod dinosaur were described by Gilmore as *Laosaurus minimus*. The locality, in the foothills of southern Alberta, was supposed to be Lower Cretaceous, but more recent studies indicate that it is Upper Cretaceous. An examination of Gilmore's type shows that it differs from the hind feet of *Laosaurus*, as well as those of all known American and Asiatic ornithopods. Closest comparison is with *Hypsilophodon foxii*, from the Lower Cretaceous of England. Temporary designation of Gilmore's species as "*Laosaurus*" *minimus* is proposed.

IN 1923 Dr. C. H. Crickmay was conducting a geological survey in the vicinity of Crowsnest River in southwestern Alberta, as part of a general investigation of the southern Alberta plains and adjacent foothills (Williams and Dyer, 1930). During the course of this work some small vertebrate remains were discovered in Cretaceous rocks about 3 miles east of Burmis station on the Crowsnest branch of the Canadian Pacific Railway. The rocks at this locality were at that time referred to the Blairmore formation, of Lower Cretaceous correlation. Dr. Crickmay called this discovery to the attention of the then Director of the Geological Survey of Canada, but such was the lack of interest at that time in palaeontological research that permission was readily granted for the specimen to be collected for the University of British Columbia. No criticism, but only praise, must be accorded Dr. Crickmay, and the University of British Columbia for collecting and preserving this specimen, which might otherwise have been lost.

The fossil material, consisting of the left hind foot, parts of the hind limb, and a few vertebrae, was submitted to the late Mr. C. W. Gilmore, of the United States National Museum. The material was adequately described and figured by Gilmore (1924A), who made it the type of a new species of *Laosaurus*, which he named *L. minimus* in reference to the extremely small size. Gilmore naturally accepted the stratigraphical data and the Lower Cretaceous reference on their face value, and this may have had some influence in leading him to compare the specimens with Late Jurassic ornithopod dinosaurs. In 1931 the Alberta geologists Dr. J. A. Allan and Dr. R. L. Rutherford (1932) conducted geological investigations in the eastern end of Crowsnest Pass, and came to the conclusion that the belt of rocks east of Burmis, identified and mapped as Blairmore formation by Crickmay, were actually Upper Cretaceous and represented the so-called Belly River formation, or more correctly, a lower portion of the Allison. Not only were there good stratigraphical and lithological reasons for thus revising the determination, but, as pointed out by those authors, the occurrence of dinosaur remains in the "Belly River" of the foothills is not unusual, whereas no other dinosaur fossils had ever been discovered in the Blairmore. This revision of the age of *Laosaurus minimus* suggested that reconsideration of the biological relationships would be very much in order. However, an opportunity to do this has not been available until recently. In 1946 Professor M. Y. Williams, of the Department of Geology and Geography, University of British Columbia, requested the writer to have Gilmore's type specimen prepared for museum exhibition, and in acceding to this request the writer asked the privilege of studying the specimen and publishing his findings. To this Professor Williams readily agreed, and the present note is offered as the result of this study. Unfortunately, no very definite conclusions can be reported.

Gilmore's account of the material is entirely adequate, and his figures are good, so

that a general account of the specimen may be omitted here. The most outstanding features of the material are the very small size and the extremely slender proportions. The left hind foot, which is almost complete, is characterized by long and slender metatarsals, which show no evidence of the presence of a fifth digit. The phalanges are short but delicate, and the unguals, although triangular and bluntly pointed, are not laterally compressed or curved and obviously bore small hoofs rather than claws. As noted above, Gilmore's comparisons with the species of *Laosaurus* from the Morrison of the western United States may have been suggested in part by the supposed early Cretaceous age of the Burmis specimen. The genus *Laosaurus* is very inadequately known (Marsh, 1894), although good material is present in the Yale Peabody Museum. As far as can be learned, the hind foot in this genus retains a vestigial fifth metatarsal, which appears to be absent in "*Laosaurus*" *minimus*. For this reason, and also because of the late Cretaceous date now assigned to the Burmis specimen, it seems very unlikely that the genus *Laosaurus* is actually represented. There is, of course, no doubt as to the general relationships of the "*Laosaurus*" *minimus* type; it obviously pertains to the ornithopod dinosaurs, and represents one of the families characterized by small, slender forms, as distinct from the larger, heavier Iguanodontidae and Hadrosauridae. But among the various known Cretaceous ornithopods, particularly those from the Late Cretaceous of North America, the comparisons with "*Laosaurus*" *minimus* are not particularly good. Along with the general characters which are found in all of the light-limbed ornithopods, the Burmis specimen shows an unusually small size and very slender and graceful proportions. Of the various American smaller ornithopods, the species of *Thescelosaurus* (Gilmore, 1915) are the best known, but in this genus the hind foot, and the limb in general, are much heavier, and the metatarsals are relatively short and stocky. *Thescelosaurus* is characteristic of the Lance formation and is found in the equivalent portion of the Edmonton formation of Alberta. From the lower, pre-Lance portion of the Edmonton formation Parks (1926) described a skeleton which he referred to *Thescelosaurus* under the specific name *T. warreni*, but more recently C. M. Sternberg (1940) has pointed out certain important differences between this and typical species of *Thescelosaurus*, and has proposed for Parks' species a new generic name *Parksosaurus*. In this the hind foot is more slender than that of the typical *Thescelosaurus* but not as small and slender as in the case of "*Laosaurus*" *minimus*. Furthermore, the ungual phalanges of *Parksosaurus* are almost unique, in that they are laterally compressed, curved, and distinctly claw-like. Another important member of the light-limbed ornithopod line is the dinosaur *Stegoceras*, which combines an enormously thickened cranium with a rather orthodox ornithopod skeleton. The best-preserved specimen of this dinosaur is in the collection of the University of Alberta, and was described by Gilmore (1924B) under the name *Troödon validus*, but the reference to the genus *Troödon* is no longer tenable (Sternberg, 1945; Russell, 1948), and Lambe's generic name *Stegoceras* must once more be applied. The University of Alberta specimen consists of a perfect skull with incomplete skeleton, from the Oldman formation of the Red Deer River valley, and thus is older geologically than *Parksosaurus* or *Thescelosaurus*. In the revised stratigraphical determination of the locality of "*Laosaurus*" *minimus* the age of this species and that of *Stegoceras validus* would be about the same. In the *Stegoceras* skeleton the metatarsals are not perfectly preserved, but they appear to be proportionately shorter and heavier than the corresponding bones in "*Laosaurus*" *minimus*. The phalanges, however, and especially the unguals, are very similar to those of the Burmis dinosaur.

Leaving North America, we find the light-limbed ornithopods represented in the presumed Lower Cretaceous of Mongolia. From the Oshih formation Osborn (1924) described *Psittacosaurus mongoliensis* on a nearly complete skeleton, and from the Ondai Sair formation the same author described *Protiguanodon mongoliense*. The two skeletons are so similar in anatomical details that there is a strong suspicion of congeneric relationships. Be that as it may, the preliminary descriptions of the two skeletons indicate that the metatarsals are considerably

heavier and relatively shorter than those of "*Laosaurus*" *minimus*. The Lower Cretaceous Wealden formation of the Isle of Wight, in southern England, has yielded the remains of the small, slender ornithopod *Hypsilophodon foxii* Huxley, known from good material in the British Museum (Natural History), and described in detail by Hulke (1883) and Swinton (1936). *Hypsilophodon* displays the closest resemblance to the "*Laosaurus*" *minumus* material of any Cretaceous ornithopood known to the writer In absolute size *Hypsilophodon foxii* is slightly smaller than "*Laosaurus*" *minimus*, but shows the same slender proportions, especially in the length and breadth of the metatarsals. Careful comparison of Gilmore's figures with Hulke's lithographs of the hind foot of *Hypsilophodon* shows that the resemblance of the individual bones is very close, although there are certain differences in the proportions of metatarsals to phalanges. There seems to be no other possible conclusion, however, than that the nearest approach to the structure of the hind foot of "*Laosaurus*" *minimus* is to be found in the hind foot of *Hypsilophodon foxii*.

In view of the wide geographical separation of the localities of *Hypsilophodon foxii* and "*Laosaurus*" *minimus*, it would not seem wise to refer the Canadian species to the Wealden genus. It is most likely that the Burmis specimen represents an undescribed genus, for the diagnosis of which it is not adequate. Pending the discovery of a more complete specimen in the "Belly River" strata of the foothills, or in the Oldman formation of the Alberta plains, it would seem that the best working arrangement would be to designate the Burmis specimen as "*Laosaurus*" *minimus* Gilmore, as has been done throughout most of this paper.

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JOURNAL OF PALEONTOLOGY, VOL. 23, NO. 5, PP. 521–535, PL. 85, 5 TEXT FIGS., SEPTEMBER 1949

ALZADASAURUS PEMBERTONI, A NEW ELASMOSAUR FROM THE UPPER CRETACEOUS OF SOUTH DAKOTA

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ABSTRACT—*Alzadasaurus pembertoni*, a new elasmosaurid plesiosaur, is described from the Sharon Springs member of the Pierre formation near Iona, South Dakota. Details of the osteology, as well as some of the associated gastroliths, are figured.

INTRODUCTION

THE specimen which forms the subject of this paper was found on the banks of the Missouri River by Mr. Arthur Salzmann, a rancher living eight miles northeast of Iona, South Dakota. His letter, dated July 23, 1945, to the Museum of Geology, South Dakota School of Mines and Technology, stated that several large fossil vertebrae had been exposed by erosion "on a slight slope of shale and are all in a line together" and that many others were uncovered by pushing away some of the shale with a stick. He also was emphatic in his belief that most of the skeleton must still be in the rock and that "all of the backbone should be there."

At this time Dr. and Mrs. Ralph Pemberton of Paoli, Pennsylvania and Mr. E. Curzon Poultney of Gwynedd Valley, Pennsylvania were spending their fifth consecutive summer in the Black Hills, during which time they had visited numerous fossil-collecting localities. Because of this general enthusiasm for paleontology, and inasmuch as their interest was especially keen for Cretaceous reptiles, they took Mr. Bump to the site of the find. The 300-mile trip by car, motorboat, and on foot seemed rather unimportant when, after a brief survey, it appeared very probable that a nearly complete skeleton of a large plesiosaur lay intact within the shale.

The skeleton was collected about two months later by Mr. Bump and Mr. Harold E. Martin, Chief Preparator of the Museum of Geology at Rapid City.

Many different individuals have contributed to the success of collection, preparation for study and exhibition, and final study and description of the skeleton; and to each of them goes personal thanks. We want especially to extend gratitude to Mr. Arthur Salzmann for reporting the discovery, and to thank him and his son for their labor during collecting operations and for the use of their motorboat for transportation. We are most grateful to Dr. Ralph Pemberton, M.D., Graduate School of the University of Pennsylvania, for his assistance in securing this specimen which is named in his honor.

Harold E. Martin has prepared and mounted the skeleton for exhibition in a skillful manner.

GEOGRAPHIC AND GEOLOGIC OCCURRENCE

The skeleton was discovered in the central part of South Dakota, 25 miles south of Chamberlain and 11 miles northeast of Iona. It was lying directly southwest of the northern tip of Bailey Island, 300 yards west of the Missouri River banks and about 70 feet above the river level at low water stage. Its location, soon to be flooded by the waters of Fort Randall Dam, was in Lot 2, Sec. 17, T. 102 N., R. 71 W.

The specimen was imbedded near the base of the Upper Cretaceous Pierre shale in the Sharon Springs member.

The Sharon Springs is composed largely of dark gray to black shales and is divisible into two zones on the presence or absence of fish remains. The lower part, called the Fish Scale zone, consists of a dark-gray, fissile, somewhat bituminous shale that always exhibits an abundance of fish scales and fragmentary fish skeletal remains. The top of the Fish Scale zone is marked by a thin layer of small, white, hard concretions. The upper part, known as the Upper Shale zone, has no fish fossils; and it is usually

darker in color and generally contains small specks of red hematite. This zone is also somewhat less resistant to weathering than the lower one. The plesiosaur skeleton was found just a few feet above the base of the Fish Scale zone.

The outcrop was formed from a rather

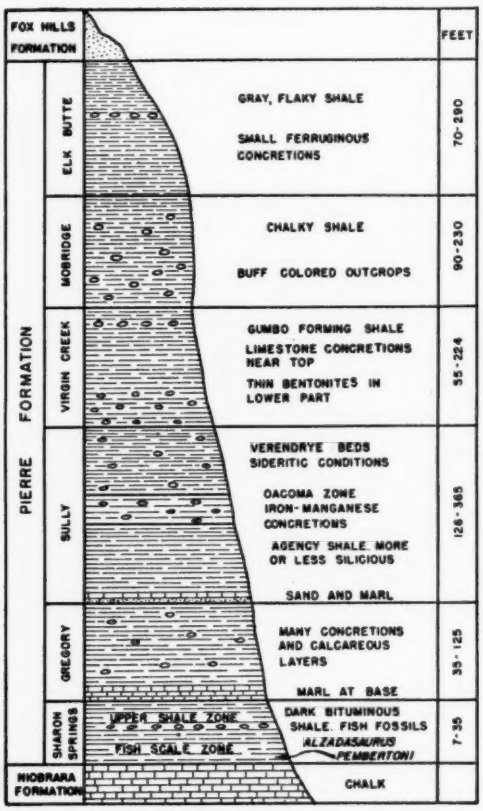

FIG. 1—Generalized stratigraphic section of the Pierre Formation. Modified from Gries and Rothrock 1941.

isolated, low-sloping, northward-facing knoll at the base of which was eroded a deep gulley. The top of the knoll merged into a small, grass-covered flat that reached to the river where it plunged downward to the river bed in a vertical cliff. The vertebral column of the skeleton extended parallel with the north face of the outcrop.

Typical Sharon Springs characters were found above and below the skeleton,—impure and reddish stained selenite in veinlets, crystal clusters, and isolated masses and yellow or golden ochrous "bloom" along the bedding planes of the shale or as loosely-cemented masses. The weathered shale surface was of a light gray color, but the unweathered rock in the quarry was dense black. A thin, three-inch layer of bentonite partially enclosed several of the bones, and about twelve feet below was another bentonite bed nearly two feet thick. During the excavation operations fragmentary fish remains were continually being uncovered; most of these were isolated vertebrae although several articulated sections up to thirty inches in length were found.

PRESERVATION AND ASSOCIATION

The skeleton was little disturbed from its original articulated position. The vertebral column formed a continous series although a few of the anterior dorsal vertebrae had been turned over or upended. The neck was bent gently backwards with the first seven cervical vertebrae offset some four feet, but still articulated with the skull. A small gully had been carved by erosion through the caudal region and all but the first four of these vertebrae were lost. The pelvic and pectoral girdles were found in approximately true position, and many of the ribs were either articulated with the vertebrae or were closely associated with them. The right side of the skeleton had been little affected by weathering as it lay deeply buried; but the left side suffered considerably from erosion and chemical weathering; and many of the vertebral processes were destroyed by these agencies. Several of the elements have been somewhat distorted by compression.

The following are completely lacking: left scapula, left radius, left ulna, right femur right tibia, right fibula, 26? caudal vertebrae about one-third of the dorsal ribs, nearly all of the left pectoral paddle and left pelvic paddle, most of the cervical and ventral ribs.

GASTROLITHS

A number of rounded stones that are, without doubt, stomach stones or gastroliths were found immediately in front of the pelvic girdle in a concentrated area about thirty inches square and seven inches deep. None of these were found outside of this

small region, and there are no similar stones in the formation. They lay mostly below the dorsal vertebrae, but several were found above and were pressed firmly against the bone.

There are 253 gastroliths having a combined weight of 8249 grams. The largest weighs 580 grams; the longest stone measures 128 mm. and the shortest 11 mm.; 41 have lengths less than 20 mm. and nine exceed 85 mm.

The matrix surrounding the pebbles was more solid and hard than elsewhere as it contained considerable iron oxide which, acting as a strong cement, made it possible to remove the stones with the matrix in blocks. Mr. George F. Sternberg of Kansas State Teachers College (oral communication, 1945) has commented on the persistence of a more firmly cemented matrix surrounding the gastroliths in the plesiosaur specimens he has examined in the field.

Of interest, too, are the many flattened, squeezed, and fractured quartzitic pebbles. This condition was apparently brought about by compression from the weight of the overlying rocks although it is difficult to understand how such resistant material, imbedded and weakly confined in clay, could suffer so much deformation by pressure exerted from a single direction.

Careful examination of each of the pebbles reveals them to be composed largely of quartzite; about 15 per cent are fine-grained pink quartzite and nearly all of the remainder fine to coarse-grained gray quartzite. There are eleven dense, black, flint-like pieces, two flat siltstones and one large and six small pieces of sandstone. The black pieces exhibit a dull luster; the others have been worn smooth but are drab and show no luster or polish.

There are no granitic pebbles such as reported found with *Alzadasaurus* by Riggs.

As these gastroliths are composed of materials of a common sedimentary variety, it is obvious that their original source could never be traced. In all probability the animal was many scores of miles from any shoreline at the time of its death.

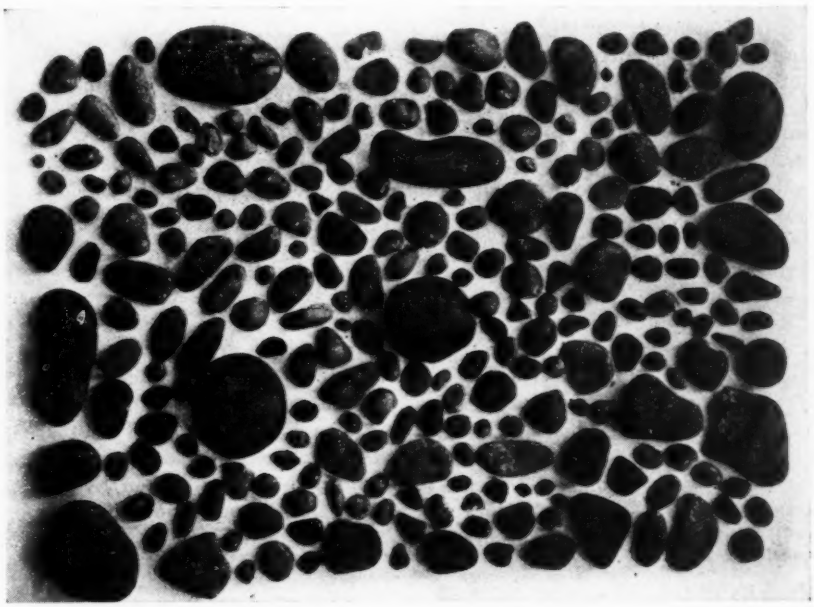

FIG. 2—253 gastroliths found concentrated in a space 30 inches square and 7 inches deep immediately in front of the pelvis. Nearly all are of quartzite and exhibit no polish. Only the black stones show a dull luster. $\times\frac{1}{7}$.

Family ELASMOSAURIDAE

ALZADASAURUS PEMBERTONI Welles and Bump, n. sp.
Plate 85; text figures 3–5

Type.—A nearly complete skeleton in the Museum of Geology, South Dakota School of Mines and Technology, No. 451.

Age.—Basal Pierre formation, Upper Cretaceous.

Diagnosis.—Related to *A. riggsi*, but with more expanded ventral plates and narrower dorsal processes of scapulae; coracoids shorter along midline suture and much more expanded posteriorly: ischia longer and with narrower posterior ends; epipodials relatively shorter compared to humerus and absolutely smaller.

Named in honor of Ralph Pemberton, M. D., whose ardent enthusiasm for vertebrate paleontology was responsible for the collecting of this and other important Cretaceous reptiles.

The skeleton is certainly adult because of its large size and the complete ossification of limb bones and girdles. This is significant as it proves that the median bar of pectrum and pelvis, absent here, but present in *Elasmosaurus*, is a valid character, not merely ontogenetic.

The *skull* is crushed flat and has suffered much from gypsum, but a satisfactory restoration was made. It measures 37.5 cm. from tip of snout to end of condyle, 14.8 cm. from snout to orbit. From snout to back of naris is 13.7 cm. but the front of the naris is uncertain. The squamosal-quadrate arch is about 17.5 cm. from condyle to top. The sagittal crest was evidently low.

There is a sharp constriction just in front of, and completely encircling the condyle, isolating it from the anterior part of the basioccipital. The floor of the braincase narrows to 1 cm. between the sutures for the exoccipitals. A depression, possibly the sella turcica, lies 7.5 cm. ahead of the condyle.

The palate is apparently preserved without crushing, but is largely obscured by skull roof above and lower jaws below. The interpterygoid vacuity is 7 cm. long and 3 cm. broad, and divided by a relatively broad parasphenoid 1.2 cm. across. The parasphenoid lies 1 cm. below the condyle and extends forward 10.7 cm., where it is broken. This palatal bar of the parasphenoid is much broader than in other skulls known to us.

The quadrate ramus of the pterygoid is crushed. The palatal ramus, lateral to the interpterygoid vacuity is relatively slender, only 1.5 cm. across near the ectopterygoid. The basisphenoid is crushed into the interpterygoid vacuity from above so as to close it.

Teeth.—There are fifteen teeth in the right upper jaw. Three of these are in the premaxillary, the fourth at the suture with the maxillary, and the rest in the latter bone The last four teeth are very small, only about ½ cm. in diameter. The largest measures 1 cm.

The right dentary bears 17 teeth, about the same size as those of the upper series. The fifth is represented by a new tip just emerging from the alveolus. It is rounded and covered with a smooth, unstriated enamel cap.

Upper and lower teeth alternate and overlap as is usual in elasmosaurs.

Vertebrae.—There are sixty-one cervicals, including the fused atlas-axis. As usual, the anterior cervicals seem much too small to belong to such a large animal. Anterior and medial cervical centra are longer than high or broad, and broader than high. This relationship holds until the last ten cervicals when the breadth exceeds the other two dimensions, followed by the length.

The rib facet rapidly ascends the side of the centrum on the three pectorals, and is extremely compressed anteroposteriorly. The breadth of the centrum is greater than the

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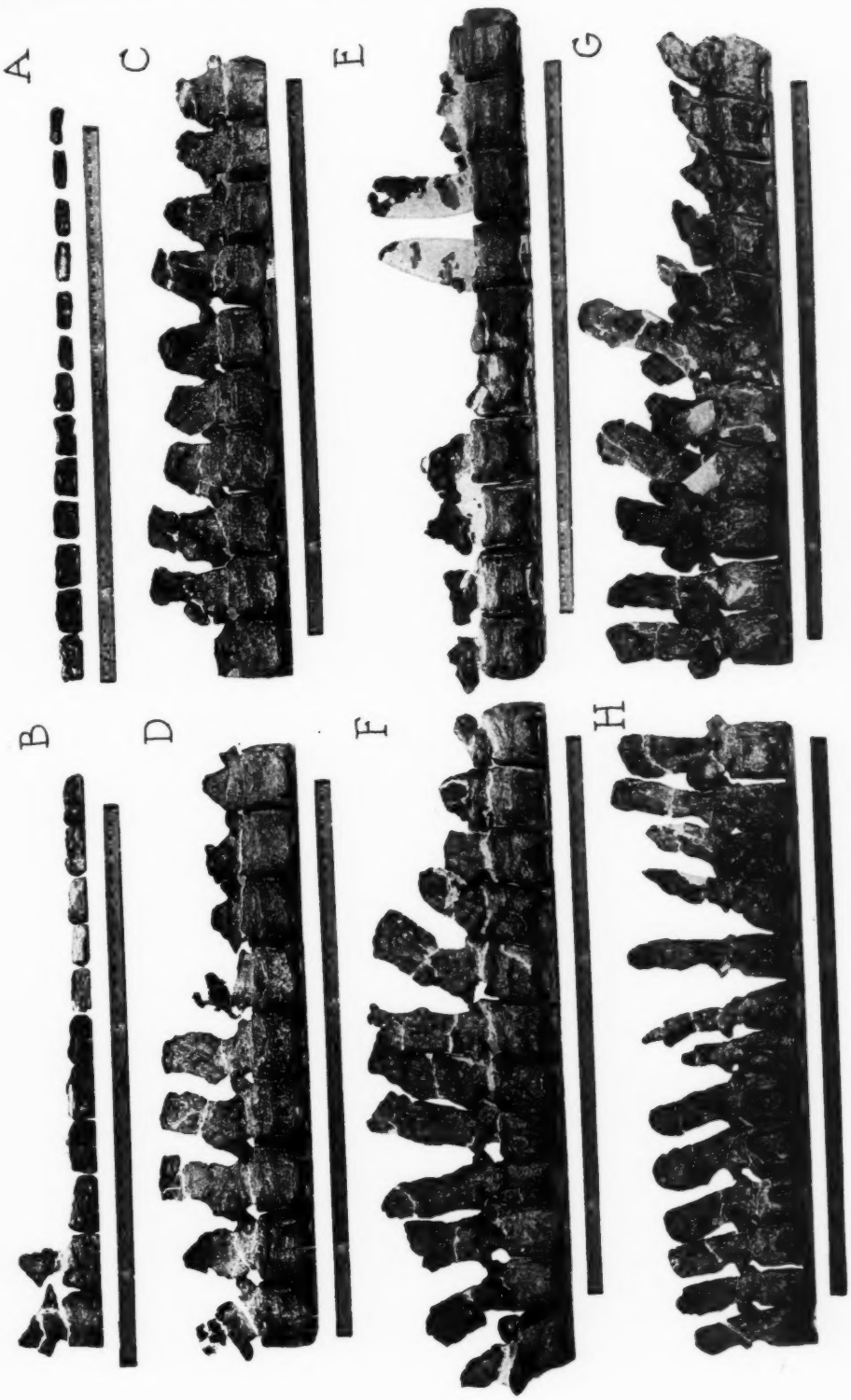
EXPLANATION OF PLATE 85

FIGS. A–H—Vertebral column of *Alzadasaurus pembertoni*. Scale shown in inches, vertebrae numbered from upper right, cervicals 13 to 6; 24 to 14; 34 to 25; 43 to 35; 53 to 44; 60 to 54, pectorals 2 to 1, dorsals 3 to 1; 14 to 4; 19 to 15, sacrals 4 to 1, caudals 4 to 1. Photos S.D.S.M.T. Museum of Geology.



Welles and Bump, Cretaceous plesiosaur

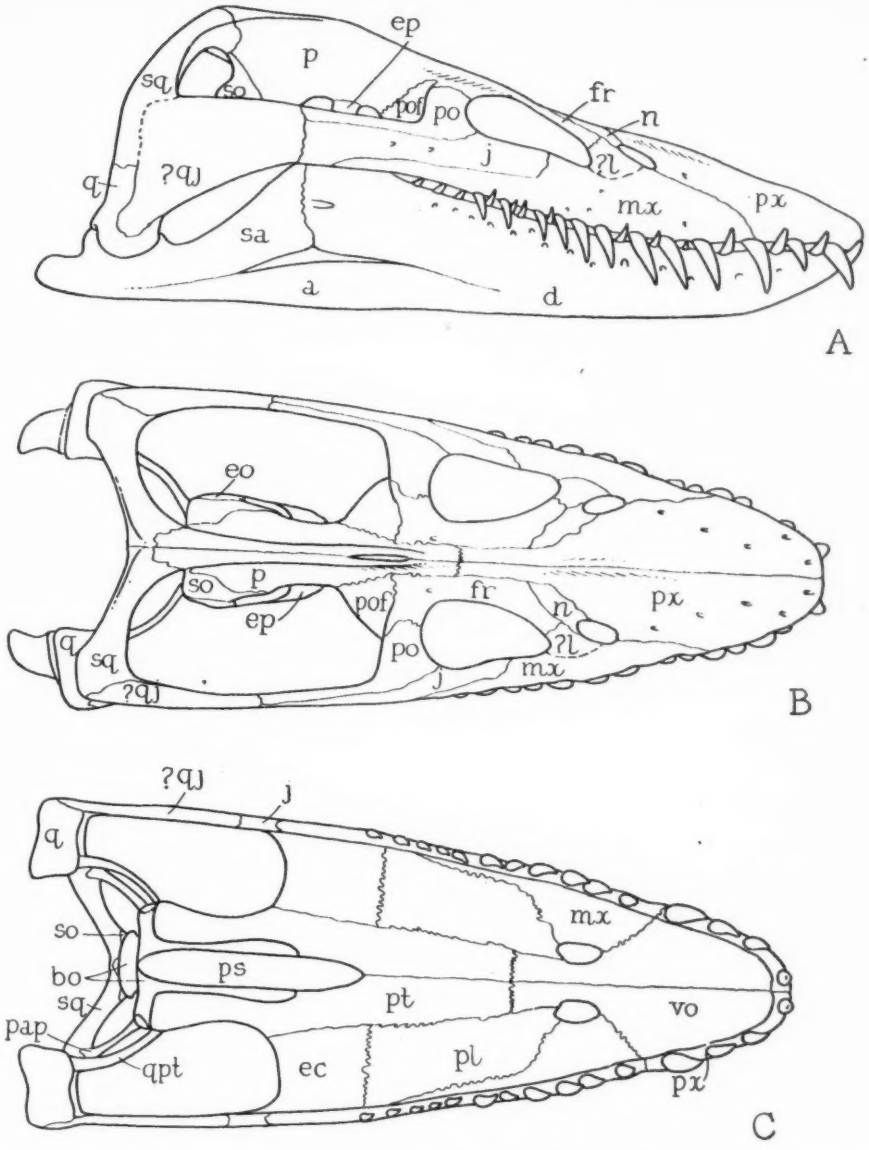


FIG. 3—Restoration of skull of *Alzadasaurus pembertoni*. The skull was first modeled in clay, natural size. Most sutures are approximated from other known elasmosaurs. *a*, angular; *bo*, basioccipital; *d*, dentary; *ec*, ectopterygoid; *eo*, exoccipital; *ep*, epipterygoid; *fr*, frontal; *j*, jugal; *l*, lacrimal; *mx*, maxillary; *p*, parietal; *pap*, paroccipital process; *pf*, prefrontal; *pl*, palatine; *po*, postorbital; *pof*, postfrontal; *pro*, prootic; *ps*, parasphenoid; *pt*, pterygoid; *px*, premaxillary; *q*, quadrate; *qj*, quadratojugal; *opt*, quadrate ramus of pterygoid; *so*, supraoccipital; *sq*, squamosal; *vo*, vomer. S.D.S.M.T. No. 451, $\times\frac{1}{4}$.

height and the length is the smallest dimension.

There are nineteen dorsals. Each bears a long transverse process with the rib facet at its tip. These processes are longest at the fifth dorsal, decreasing in size from there on. The proportions of the dorsal centra are the same as of the posterior cervicals with the breadth greater than the height, which in turn exceeds the length.

There are evidently four sacral vertebrae in which the rib facet is formed partly by diapophysis and partly by centrum. The facets on the first two are compressed and must have borne weak ribs. The last two sacrals have large rib facets and obviously provided the anchorage for two strong sacral ribs. Proportions of the centra are as in the dorsals.

The four anterior caudals complete the column and twenty-six more are estimated to be missing. Proportions are similar to those of the dorsal centra, while the rib facet descends to the lower side of the centrum on the second caudal.

The vertebral formula is thus 61 cervicals, 3 pectorals, 19 dorsals, 4 sacrals and 4(+26) caudals.

The *interclavicle* is weathered anteriorly and broken, but was not a large element. It was pointed anteriorly, concave posteriorly, and had posterolateral wings. It lay in the pectoral cartilage and could not have met the scapulae. The element is poorly preserved and although it probably represents fused interclavicle and clavicles, we cannot be sure of a possible suture on the right side.

However, the presence of this element has now been established in so many genera of Elasmosauridae that it probably occurred in all. It was a small, isolated element, easily detached from the rest of the skeleton, difficult to recognize in the field and easily lost. It is not surprising that knowledge of its prevalence has been so long delayed.

The right *scapula* is complete save for the important posterointernal corner of the ventral plate. The glenoid region is flattened a little but proportions are apparently unaltered. The coracoid facet is longer than the glenoid facet. The neck is fairly stout, 10 cm. across, as opposed to 17 cm. across the base. The dorsal process is not separable from the ventral plate viscerally, but ventrally a slight ridge runs anterointernally from the tip of the glenoid fossa. This ridge has a slight anterior concavity, so that the neck is thinned below to about 7 cm.

The upper edge of the dorsal process is concave laterally, an indication of a cartilaginous continuation. It is about 8 cm. long and 24 cm. high (from above the ventral ridge). The tip curves slightly backward.

The ventral plate is 17 cm. across its narrowest part, then broadens to an estimated 24 cm. The anterointernal angle lies about 5 cm. lateral to the inner edge of the coracoid suture. There is no indication of the median bar that characterizes the genus *Elasmosaurus*, but the scapulae could have met in the midline.

No trace was found of a clavicular impression on the scapula.

The right *coracoid* is complete in outline, but thinned by crushing. There is no evidence of a median bar as the midline projection ends over two cm. behind the inner end of the scapular suture, almost even with the front of the coracoidal part of the glenoid. The anterior concavity is pronounced. The intercoracoid vacuity has developed beyond the heart-shape of many forms, to two wings isolated by the long posterior projection of the midline.

The ventral surface bears a transverse ridge, 8 cm. thick at the midline and decreasing to 2 cm., 11 cm. laterally. This ridge is a little behind the highest part of the visceral surface.

The most outstanding character is the great expansion of the posterior plate. It increases from a 13 cm. neck to about 34 cm. posteriorly, 5 cm. broader than at the back border of the glenoid. It not only reaches the midline, but meets the opposite coracoid along a 9 cm. border.

Both *paddles* are flat, and probably aligned themselves on a bedding plane when the carcass settled to the bottom. Subsequent crushing, therefore, compressed the elements but did not distort them appreciably. The elements are arranged in rows, i.e., propodial; epipodials; proximal mesopodials; distal mesopodials+metapodial V; metapodials+phalanx one of the fifth digit; and first phalanges+phalanx two of the

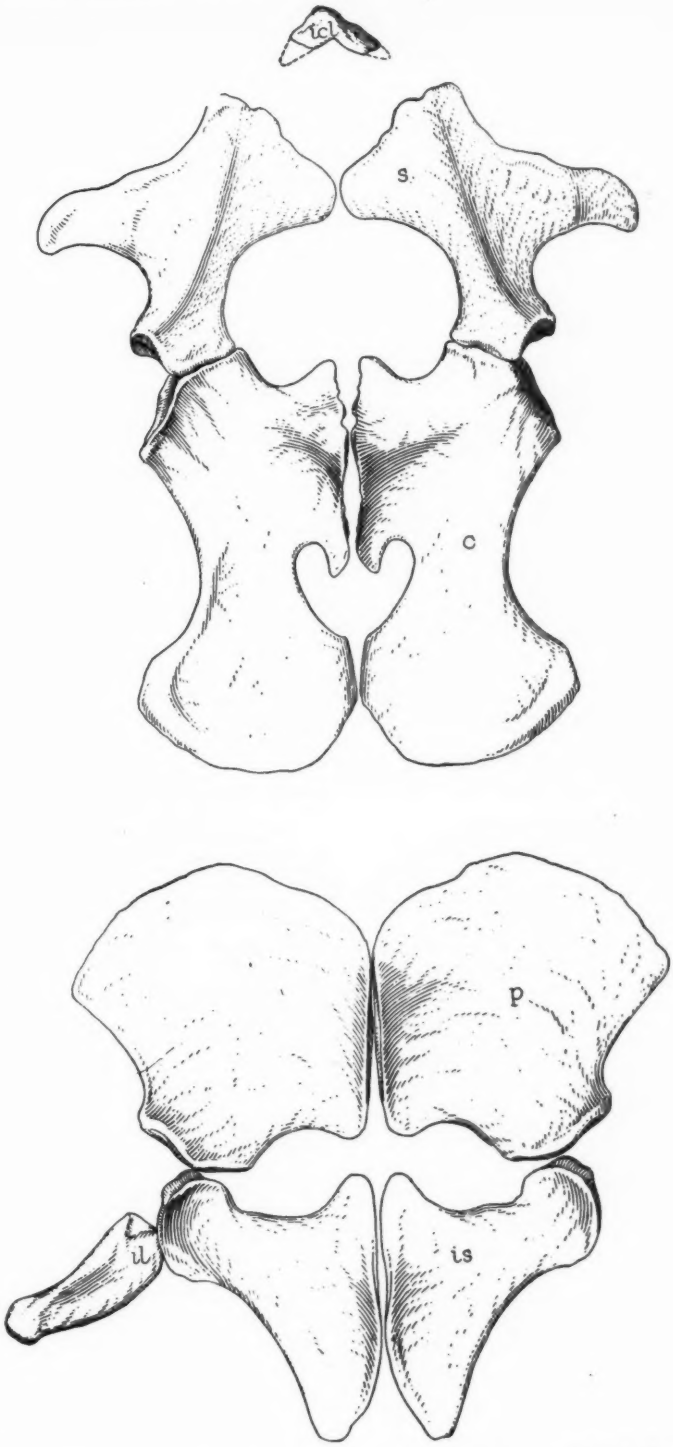


FIG. 4—Ventral views of restored pectrum and pelvis of *Alzadasaurus pembertoni*. *c*, coracoid; *icl*, interclavicle; *il*, ilium; *is*, ischium; *p*, pubis; *s*, scapula. S.D.S.M.T. no. 451, $\times\frac{1}{11}$.

fifth digit. Distally the phalanges become irregular, but this far the number in each row is 1, 2, 3, 4, 5, 5. The right front paddle is beautifully preserved in its natural position.

The right *humerus* is crushed laterally from an estimated 14 cm. to 8 cm., but the shape is only slightly distorted. The head projects forward, continuing the curve of the anterior border of the shaft. It measures 14 cm. along the top and was probably about 7 cm. wide. Both capitulum and tuberosity bore thick caps of cartilage.

The tuberosity is separated from the head only by anterior and posterior notches, with no longitudinal groove connecting these two notches. Proximal surfaces of both heads are approximately parallel to the distal end of the humerus. The tuberosity begins 6 cm. behind the capitulum and projects two cm. posteriorly, having a length of 9 cm.

The anterior "knee" is poorly developed at the distal end, and is quite thin, as usual with elasmosaurs. In this form a distinct posterior knee is also developed.

Distal facets for epipodials are deeply concave, that for the radius being 12 cm. long and 1.5 cm. deep, for the ulna 9.5 cm. long and 1.5 cm. deep.

The distal breadth is 70% of the length, a little more massive and therefore more advanced than *A. riggsi* with a figure of 64% (erroneously given as 80% in Welles 1943, table 14).

The anterior epipodials not only meet, but almost fuse. The epipodial foramen is reduced to a horizontal oval 1.5 cm. high and 2.4 cm. long.

The *radius* is crushed from an estimated 5 cm. thick to 4.3 cm. It is wider than long, and all borders except the ulnar are convex. A slight concavity on the anteroventral border is due to crushing against an unyielding object below. The facets for radiale and intermedium are not distinct, but are a part of the continuous distal border.

The *ulna* is also crushed so its original thickness is not evident, although it probably was less than the radius. It is nearly circular from the epipodial foramen, proximally, posteriorly and distally to the intermedial facet. This, and the lower anterior projection to meet the radius, extend beyond the circular outline.

The *radiale* has a proximal facet for the anterior ¾ of the radius, a posterior facet for the intermedium, and a small distal facet for the second carpale. It is rounded anteriorly without a proximal anterior projection.

The *intermedium* meets the radius and ulna with approximately equal facets, the ulnar slightly larger. Distally, the facet for the second carpale is larger than for the third (carpale 4).

The *ulnare* is broken posteriorly. Its distal face is about equally divided into facets for the third carpale (carpale 4) and metacarpal V.

The first *carpale*, carpale 1, lies distal to the outer two-thirds of the radiale. Its distal facet is for metacarpal I, and it bears a posterodistal facet for mc. II. The second carpale, c 2, meets the radiale and intermedium proximally, with its larger facet against the latter. Thus the thrust line from the posterodistal end of the humerus through the ulna, intermedium and carpale 2 is pronounced, although not so broad as in *Aphrosaurus* and *Morenosaurus*. The distal facets for metacarpals II and III are unequal the larger being posterior.

Carpale 4 (the third carpal element (see Welles, 1943, p. 143)), is almost a mirror image of the second, with a larger proximal facet for the intermedium and a smaller posterior facet for the ulnare. It is broader than long in contradistinction to that of the rear flipper, which is longer than broad.

Metacarpal V has shifted entirely into the distal mesopodial row and bears against the ulnare. Metacarpal I is short and broad. It bears only on the first carpale. The second metacarpal is the broadest of the series with its proximal end bearing on carpalia 1 and 2. The third metacarpal is the longest of the series. It bears largely on carpale 2 but partly on carpale 4. The fourth metacarpal bears only on carpale 4, and next to it lies the first phalanx of the fifth digit.

The lines between the horizontal series of the elements are zigzag from the humerus to the metacarpal series. At the distal ends of the metacarpals (and the first phalanx of digit 5), this line runs straight across the flipper. This could indicate a relatively stiff upper paddle, with a flexible line where the joints become straight. However, there must have been cartilage and connective tissue

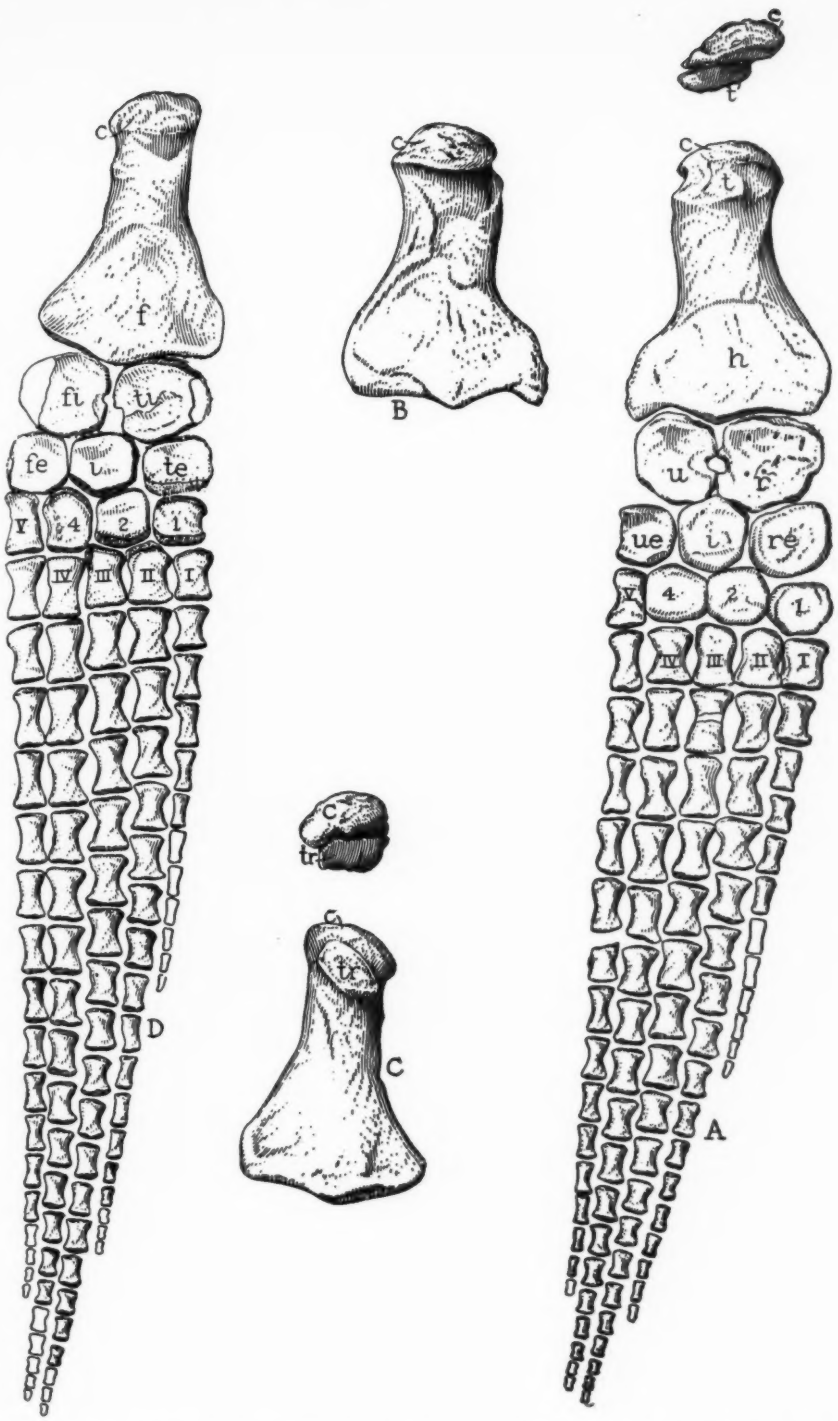


FIG. 5—Front and hind paddles of *Alzadasaurus pembertoni*. A, dorsal or anterior view of right front paddle, with proximal end of humerus above, *B*, ventral or posterior view of humerus. C, dorsal or anterior view of left femur, proximal end above. D, ventral or posterior view of left femur, tibia and fibula and right mesopodials *et seq.*

c, captulum; *f*, femur; *fe*, fibulare; *fi*, fibula; *h*, humerus; *i*, intermedium; *r*, radius; *re*, radiale; *t*, tuberosity; *te*, tibiale; *ti*, tibia; *tr*, trochanter; *u*, ulna; *ue*, ulnare; 1, 2, 3, 4, centralia; I–V, metapodials. Restored phalanges unshaded. S.D.S.M.T. no. 451, $\times\frac{1}{10}$.

between all limb elements so the flexibility may not have been determined solely by alignment of bones.

No supernumerary ossicles are preserved, but it is likely that some were present, particularly between the ulna and ulnare posteriorly.

The phalangeal formula is 5 (+6), 15 (+1), 17 (+1), 15 (+2), 14 (+1). The number in parentheses indicates the number restored by Bump, and is probably a good estimate.

The *ilium* is a stout, curved rod with a slight thickening and widening at the acetabular end. It apparently met only the ischium at the acetabulum, and that by a large facet on the ischium and an oval facet 5×10 cm. on the ilium. A narrow facet runs 4 cm. up the anterior edge of the lateral face, evidently a dorsal continuation of the acetabulum. The upper end is narrower than the lower, and shows no distinct facets for sacral ribs. The anterior border is rotated inward a bit and must have been loosely connected to the sacrum.

The sacro-iliac joint was so weak that progression on land must have been impossible.

The right *pubis* is a large flat plate with a median suture at least 28 cm. long. The anterior border is convex anterolaterally and straight anteromedially, indicating that Riggs' (1939) restoration of *Alzadasaurus riggsi* is essentially correct and Welles' (1943, fig. 30, with concave anterior border) wrong. The ischial articulation is slightly shorter than the acetabular face.

There is no medial bar from pubis to ischium.

The right *ischium* has a 28 cm. straight symphyseal border. It then curves laterally 14 cm. to a rather sharp distal point. The neck is about 11 cm. across, the lateral acetabular part is massive, 11 cm. wide and about 15 cm. long. It is crushed to about 6 cm. thick. The dorsal border of the acetabulum overhangs the ventral.

The right rear paddle is in natural articulation, but has weathered more than the front paddle.

The left *femur*, substituted for the missing right, is almost uncrushed at the middle of the shaft, but is flattened proximally from an estimated 13 cm. to 11 cm. If the femur is oriented with the anterior part of the tibial facet horizontal, the upper part of the anterior border of the shaft is vertical, and the head dips posteriorly about 20° while the dip of the trochanter is about 40°. Both heads, as with the humerus, bore thick caps of cartilage. Capitulum and trochanter are completely separated by the confluence of the anterior and posterior grooves. The anterior groove is much longer so that the junction lies just above the highest (anterior) point of the trochanter.

The articular facet for the tibia is slightly concave, 12 cm. across and 0.5 cm. deep, while the fibular facet is convex. There is a well-developed anterior knee as in the humerus, but the posterior border is concave to its distal extremity.

The left *tibia* has suffered from gypsum and crushing, but its outline is probably nearly correct. The outline of the epipodial foramen is poorly preserved, but it seems to have been much less well developed than on the forelimb. Contact with the fibula is probable above the foramen, but not below. The proximal surface fits into the anterior concavity of the femur while the distal end has a large facet for the tibiale and only a small facet for the intermedium.

The left *fibula* has but a small indentation forming the posterior border of the epipodial foramen. Its proximal surface is rounded, its posterior border sharply rounded so that wide gaps are left between the femur above and the fibulare below. These gaps were undoubtedly filled by supernumerary ossicles. The distal facet for the intermedium is flat but the fibulare facet is round. Much connective tissue and cartilage must have surrounded the epipodials.

The rest of the paddle is from the right side.

The proximal mesotarsals are about equal in length, the tibiale broader than the other two. It meets only the tibia anteriorly, tarsale 1 posteriorly, and probably just touched the anterior corner of tarsale 2. The intermedium has its greater proximal surface against the fibula, its distal facets for tarsalia 2 and 4 about equal. The fibulare is almost circular, meeting the rounded fibula proximally and supporting tarsale 4 and metatarsal V distally.

Tarsale 1 meets the tibiale proximately,

metatarsals I and II distally, the smaller facet for the latter. Its anterior border is concave. Tarsale 2 meets the intermedium proximally and may touch the tibiale. It has a smaller distal facet for metatarsal II and a larger for metatarsal III. It and tarsale 1 support the first three metatarsals.

Tarsale 4 (the third in the series) has two phalanx of the fifth digit. It has moved, as in the carpus, completely into the metapodial row and adapted its head to the more proximal mesopodial.

The digital formula, with restored parts in parentheses, is 5 (+6), 14 (+3), 17(+3), 14 (+5), 13 (+4).

Comparisons.—The fore limb is typically

TABLE 1—UPPER CRETACEOUS ELASMOSAURS OF CENTRAL NORTH AMERICA
(Correlation from Stephenson *et al.*, 1942, Bull. Geol. Soc. Amer., *53*)

Danian	Laramie		Moreno
Maestrichtian	Fox Hills		
Campanian	Pierre		
Santonian		*Alzadasaurus pembertoni* *Elasmosaurus platyurus*	
Coniacian	Niobrara	*Hydralmosaurus serpentinus* *Thalassonomosaurus marshii* *T. nobilis* *Hydralmosaurus willistoni* *Elasmosaurus snowii*	
Turonian	Benton = Eagle Ford	*Elasmosaurus morgani* *Alzadasaurus riggsi* *Ogmodirus martinii* *Thalassomedon haningtoni*	
Cenomanian	Dakota		

proximal facets, both about equal, for the intermedium and fibulare. It is longer than broad and its posterior border is concave and rounded, a character held over from its earlier external position. Distally it supports metatarsal IV only, and is about the same width as this element.

The fourth member of this series is, as in the forelimb, metapodial V. It is longer than the distal mesopodials, rounded posteriorly and meets the rounded fibulare proximally.

The metatarsals are much like the metacarpals, but are slightly smaller. Metatarsal II is the broadest. Metatarsals I, II and III are borne on the first and second tarsalia, and metatarsal IV meets tarsale 4. The posterior element in this row is the first

elasmosaurian with short propodials and shorter than broad epipodials. This, the long neck and short head and short ischia place it in the Elasmosauridae.

Alzadasaurus riggsi is close to the present form in most comparable characters. Absence of the clavicular arch is probably fortuitous. The scapulae have less expanded ventral plates and more rounded dorsal processes. The coracoids project farther forward and backward in the midline, are much less expanded posteriorly and are relatively much broader.

The pubes are probably similar. The ischia are shorter, do not extend so far forward along the midline, and have more rounded posterior tips. The humerus is

about 6 cm. shorter, and with less well developed posterior knee and less concave epipodial facets. Epipodials are longer, but the radius is the same breadth, the ulna a centimeter broader. Epipodials are, therefore, not only relatively larger compared to the humerus (more primitive), but also absolutely larger.

Taken with the proportions of the humeri, these differences are of such a nature as to clearly indicate a more primitive condition in *A. riggsi*. They might also be interpreted as indicating a more juvenile individual. However, *A. riggsi* seems to be at least a young adult and the proportional differences of propodial and epipodials are probably significant. The South Dakota specimen is closely related, and probably in the direct line of descent.

Aphrosaurus has vertebrae with deep semicylindrical grooves on the ventral surfaces of the posterior cervicals. The interclavicle is concave anteriorly, not pointed as in the South Dakota specimen. The scapula has a broader dorsal process that rises more anteriorly than in *Alzadasaurus pembertoni*. The coracoid of the California form projects much farther anteriorly along the midline and is relatively much broader than long. The posterior plates are relatively less developed and their necks more slender. The ventral thickening is in the center of the midline plate, while in the South Dakota specimen, it lies only about $\frac{1}{3}$ of the way back.

The propodials of *Aphrosaurus* show no such separation of head and trochanter as develops in this form. Differences are evident in the paddles, but enough has been enumerated to indicate that each represents a distinct kind of elasmosaur.

Elasmosaurus differs in having the pectoral and pelvic bars well developed. This was described by Cope and only recently confirmed in a second species from Dallas, Texas. This new specimen also indicates a humerus without the anterior and posterior knee, and with only slightly concave distal facets; epipodials more widely separated, and without the constricted foramen.

E. platyurus Cope, and the Dallas form both show the posterior coracoidal plates much less expanded, and the neck more slender, and a much smaller extension of the coracoids posteriorly along the midline into the intercoracoidal vacuity.

Fresnosaurus is a juvenile, quite differently proportioned, and probably not related.

Hydralmosaurus serpentinus (Cope) was fairly well described (Cope 1877), but no figures were given. Watson (1924) published a drawing of the pectrum and right paddle made by Gregory, but here the pectoral bar is erroneously indicated and the humerus is not clearly shown. Welles has recently had the privilege of studying the type material through the kindness and cooperation of Dr. E. H. Colbert of the American Museum of Natural History, and so presents the following comparisons. A detailed description is reserved for a later paper.

The coracoids of *H. serpentinus* have a great ventral keel, a convex anterior border and do not project posteriorly into the intercoracoid vacuity. The humerus has a great posterior expansion above the ulna and the ulnar facet is relatively larger than in *A. pembertoni*. The epipodial foramen is larger and the radius barely meets the ulna proximal to the foramen. The posterior border of the pubis is more concave and the pubis extends posteriorly in the midline nearly to a level with the interior end of the ischial suture at the acetabulum. The ischium is considerably stouter posteriorly and is relatively shorter along the midline. The femur differs markedly in having capitulum and trochanter continuous with only the slightest indication of their boundary. The trochanter makes nearly a right angle with the shaft. The tibia and fibula do not meet above the epipodial foramen, which is proximately situated. Metatarsal V has a concave posterior border with a round, finished surface.

Hydrotherosaurus alexandrae has a longer dorsal process of the scapula, which is markedly set off from the ventral plate, a less expanded posterior plate of the coracoid, relatively short ischia, a less pronounced separation of capitulum and tuberosity of humerus and more concave epipodial facets. The radius has a much larger facet for the intermedium, and the epipodial facet is absent. The femur lacks the pronounced separation of the heads, and the

trochanter is not inclined to the capitulum; both distal facets are convex.

Morenosaurus has a broader, larger, clavicular arch. The sharp separation of the dorsal process of the scapula is more pronounced and this process is broader. The midline meeting of the ventral scapular plates is unlike the South Dakota form. The anterior midline projection of the coracoids is very much greater and their necks slenderer. The humerus has a more pronounced separation of head and tuberosity. The anterior knee is poorly developed; the posterior absent, with a consequently sharper lower posterior border. The epipodials are separated and lack the constricted foramen. The radiale and first centrale are more pointed anteriorly. The femur shows a lesser separation of head and trochanter, a more sloping lower border, and no anterodistal knee. Fibula and tibia are relatively longer and lack the constricted foramen.

Ogmodirus martinii is a juvenile and cannot be compared. The same is true of *Leurospondylus ultimus*.

Thalassiosaurus ischiadicus has very short ischia. The distal border of the femur is nearly straight and slopes upward posteriorly. The tibia and fibula are relatively longer and the epipodial foramen is absent.

Thalassomedon haningtoni is quite different in all comparable respects. The scapulae meet in the midline, the clavicular arch is large, the propodials have confluent heads and narrow distal ends. The epipodials have angular outlines without a foramen, and there are five instead of the usual four elements in the distal mesopodial row. The ischia are broader and shorter.

Thalassonomosaurus marshii has a hu-

TABLE 2—MEASUREMENTS IN MILLIMETERS OF VERTEBRAE OF *Alzadasauras pembertoni*
(Measurements by James D. Bump)

Vertebra Number	Centrum			Vertebra Number	Centrum			Vertebra Number	Centrum		
	L	H	B		L	H	B		L	H	B
1–2	54			32	111	68	84	Pec. 1 62	96	91	146
3	33	27	36	33	110	72	84	63	84	93	144
4	40	28	45	34	111	71	81	64	90	100	153
5	45			35	111	70	89	Dors. 1 65	93	102	127
6	51			36	113	75	85	66	91	97	130
7	56			37	115	73	84	67	96	96	153
8	60			38	117	74	85	68	100	90	151
9	73			39	120	76	86	69	100	94	138
10	76			40	121	80	86	70	101	89	129
11	68	31	41	41	119	84	81	71	102	101	132
12	71	34	50	42	120	82	84	72	105	102	133
13	78	36	51	43	119	84	87	73	102	109	131
14	80	40	49	44	116	85	89	74	100	110	129
15	84			45	119	85	92	75	93	111	132
16	83			46	117	85	92	76	94	113	131
17	84			47	118	82	95	77	97	115	124
18	82			48	120	86	91	78	99	107	130
19	80			49	115	92	110	79	93	106	131
20	81			50	114	92		80	88	102	127
21	92			51	112	92	98?	81	89	100	129
22	96	43		52	114	81	123	82	96	102	130
23	98	40	55	53	110	93	110	83	90	102	123
24	103		58	54	115	93	117	Sac. 1 84	87	100	119
25	106	50	54	55	112	87	123	85	85	97	115
26	103	58	66	56	111	94	131	86	83	94	99
27	104	61	72	57	106	91	137	87	81	94	90
28	110	60	75	58	102	90	144	Caud. 1 88	73	87	104
29	109	63	80	59	104	85	135	89	76	85	101
30	108	66	85	60	98	94	140	90	70	86	106
31	111	69	86	61	97	86	144	91	70	83	102

merus with a more sigmoid shape, no posterodistal knee and an almost flat distal border. The scapulae meet broadly in he midline and project toward the coracoids.

Thalassonomosaurus nobilis differs in its relatively slender femur, the lack of an anterior knee, the supernumerary facet and the convex distal end. The scapulae met firmly in the midline.

TABLE 3—MEASUREMENTS IN CENTIMETERS OF APPENDICULAR SKELETON OF *Alzadasauras pembertoni*.

Clavicle	
Width of both	42
Length, parasagittally	20
Scapula	
Greatest length, anteromedially from glenoid	40.5
Midline to notch of dorsal proces	29
Width of glenoid bar	10
Width of dorsal process	10
Height of dorsal process	25
Anteromedial from lateral end of coracoid suture	37
Length of glenoid portion	8.5
Length of coracoid suture	11
Coracoid	
Greatest length, parasagitally, from inner end of scapular suture	62
Length of midline suture	32
Length of scapular suture	11
Length of glenoid portion	12
Greatest width at posterior edge of glenoid	31
Width at front of scapular suture	12
Width of shaft	13
Width of posterior expansion	35
Humerus	
Anteroposteriorly proximally	14
Same, shaft	12
Same, distally	26.5
Greatest length	38
Radius	
Length	12.5
Width	14
Total length front paddle, including humerus	166
Ulna	
Length	12
Width	11
Ilium	
Length	27
Anteroposterior proximally	7.6
Same, distally	10
Width distally	5+
Pubis	
Greatest length parasagittally	45.5
Length, midline suture	27
Greatest width	46
Ischium	
Anteroproximally at glenoid	14
Same, distally	40
Same, shaft	11
Breadth from midline	32
Femur	
Length	36.5
Anteroposterior proximally	12
Same, shaft	9.5
Same, distally	24.5
Tibia	
Length	10.5
Width	13
Fibula	
Length	12
Width	12±
Total length hind paddle, including femur	173

Many recorded occurrences of "gizzard stones," often with fish remains, testify to their manner of reducing prey to assimilable size.

The "gizzard stones" relieved the head of all masticatory responsibilities, leaving it free to dart after the prey, snap it up, and start it down the long neck. The creature could thus devote his full time to fishing,

HABITS

In common with other elasmosaurs, *Alzadasauus pembertoni* was undoubtedly a highly efficient fish-catcher. The long, sharp teeth were set along the edges of jaws that evidently gaped wide, yet were held in strict alignment by the deep articular sulcus. This multi-pronged trap, set on a long, flexible neck, was obviously highly successful, for it lasted from Triassic pistosaurs through Cretaceous elasmosaurs with a general ten-fold increase in size.

and wasted none on ingestion.

His paddles are highly specialized oars. The great development of the head of the propodials indicates a considerable use of these powerful propelling mechanisms. They were undoubtedly "feathered" on the return stroke, then turned with the leading edge down for the propulsive stroke. It has been shown before that the animal had a flexible, streamlined body and that normal locomotion was probably undulatory, the paddles used primarily as starters and for

sudden acceleration. The relatively short, stout tail undoubtedly was a powerful organ of propulsion.

The paddles were also efficient brakes as shown by the well defined propodial tuberosity and trochanter. These are the bearing surfaces for a back-water stroke and their extreme development in *Alzadasaurus pembertoni* is indicative of an animal that could stop, turn, or back up with agility.

The extreme specializations of the paddles rendered them practically useless for progression on land. This has led me to suggest that the elasmosaurs probably spent their entire lives in the water and were incapable of returning to land. This is given further credence by the rod-like ilium and its weak attachment to the sacral vertebrae. We would, therefore, expect the elasmosaurs to have been ovoviviparous as were the ichthyosaurs. They were highly specialized reptiles, world-wide in distribution and, geologically speaking, a long-lived stock.

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THE SUBSPECIES OF *HOPLOPHONEUS:* A STATISTICAL STUDY

JEAN HOUGH

ABSTRACT—A statistical study was made of nineteen specimens of *Hoplophoneus* collected from the lower Brule of Niobrara County, Wyoming and now in the U. S. National Museum, Washington, D. C. The results were compared with those of a similar study made by Simpson with specimens from approximately the same horizon in South Dakota, and with data obtained from other *Hoplophoneus* specimens in museums throughout the country. Comparison was also made of the cranial variation in these specimens with that of the North American subspecies of *Felis concolor*. From these studies it was concluded that all of the *Hoplophoneus* specimens from the Brule are one species but that this species is divided into a number of geographical subspecies, one of which *Hoplophoneus primaevus primaevus* is represented by the majority of specimens collected from South Dakota and another, *H. primaevus latidens*, represented by the nineteen USNM specimens from Wyoming and Thorpe's types of *H. marshi*, *H. latidens* and *H. molossus* from Colorado and Nebraska. There was also a very large subspecies which probably inhabited a different locality from either of these but is represented in the South Dakota and Wyoming collections by a few skulls and jaws referred to *H. occidentalis*. There is also some evidence of a very small subspecies of which *Hoplophoneus belli* of the Sespé of Las Pasos Hills, California may be a survivor.

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INTRODUCTION

DISCONTINUOUS variation is a fact of the organic world. If this were not so, an hierarchial system of classification would be purely subjective and the best classification, as Dobzhansky points out, a "sort of multidimensional periodic system with a number of dimensions equal to the variable genes." (Dobzhansky, 1947, p. 367) The basic unit in the hierarchial system is the species since it is in species formation that discontinuity first occurs. Some isolation, geographic, ecological, or physiologic separates a hitherto freely interbreeding unit into two or more such units, each reproductively isolated, and permits accumulation of gene differences which, in time, become sufficiently great to be expressed as morphologic differences. The species therefore, is a "natural" category in a sense that the higher categories are not, and it is the only one capable of experimental verification. In fossil groups, of course, proof of interbreeding or the absence of it is impossible experimentally. Even in recent populations, however, few specific determinations are based on experimental proof of genetic isolation. Morphological distinction coupled with evidence of ecologic or geographical isolation is usually considered sufficient evidence that a given population is distinct.

Much the same criteria usually used in the determination of living species are available for fossil species, at least among mammals. There are, of course, certain limitations. Fossilization is an accident. The specimens accumulate only under favorable conditions and over a period of time, always long in terms of recent events. The samples thus made available to paleontologists are drawn usually from populations covering a much wider area than the site of fossilization and perhaps not contemporaneous. Paleontologists are thus forced to rely to a far greater extent than neo-zoologists on morphological characters as a sole means of distinction.

The taxonomic situation is further confused by the fact that collections of any fossil group are made over a period of years. When the first descriptions are published only a few specimens are known and there is a quite natural tendency to consider each specimen a new species. This is unavoidable and is better in the writer's opinion than not describing a new form at all or indiscriminately lumping it with an older species which may be quite different. There comes a time, nevertheless, when multiplication of species by this method ceases to serve any useful purpose and more accurate determination is possible and necessary.

Statistical methods of comparing two small samples with each other, and single specimens with larger samples have been discussed in detail by Simpson, in Simpson and Roe (1939) and in several shorter papers (especially Simpson, 1941 a). The first application of these methods to the very complicated taxonomy of *Hoplophoneus* was also made by him (Simpson, 1941). In this paper, which is extremely important both from the standpoint of its conclusions and methods, Simpson shows by an analysis of a series of continuous variates representing the usual standard measurements, and by a number of indices, also in common use, that four species previously considered distinct, *H. oreodontis*, *H. primaevus*, *H. robustus* and *H. insolens*, are in fact, one species, *H. primaevus*, since this name has priority. The characters which had been described as specific distinctions are, according to this determination, differences due to age and sex. *H. oreodontis* as it has been described, is made up of two different types of skulls. The neotype, AMNH no. 5338 and AMNH no. 9764 are young individuals. Sutures closed or closing in other specimens are open in these. The short face, rounded cranium, horizontal profile of the skull, lack of development of the sagittal and occipital crests are all juvenile characters. The permanent teeth which have just erupted and are entirely unworn are large, absolutely and relatively. In fact, the cheek teeth are in the upper brackets of the values for *H. primaevus* and within the range of *H. robustus*. When mature this individual would have been a large *H. primaevus* or small *H. robustus*.

On the other hand, Princeton Museum no. 13628 and no. 10515 and AMNH no. 38890, the smallest specimens are not young individuals. AMNH no. 38890, the smallest, is also the oldest. The skull and tooth dimensions are smaller than those typical of *H. primaevus* although within the possible range of that species, Simpson considers these small females. To summarize: part of the *H. oreodontis* specimens are young individuals, part are small females; the *H. primaevus* specimens including Leidy's hypodigm are moderate sized to large females; *H. robustus* and *H. insolens* are moderate size to large males.

Simpson also discusses Thorpe's species, *H. marshi*, *H. molossus* and *H. latidens*, briefly but, since there was only one specimen known for each at the time, reaches only tentative conclusions as to their status. A collection of *Hoplophoneus* specimens in the U. S. National Museum offers an almost unique opportunity for extending Simpson's studies and reaching more definite solutions to some of the problems raised in his paper, expecially as to the status of *Hoplophoneus molossus*. The specimens in question consist of a series of nineteen exceptionally well preserved skulls all associated with some limb bones and several with almost complete articulated skeletons. They were collected by Mr. George Pearce in 1942 from the Lower Brule of Niobrara Co., Wyoming, a few miles on either side of Little Indian Creek near the northwest corner of Walker Ranch. The skulls form a graded series as to size. The smallest are only slightly larger than the neotype of H. *oreodontis*, the next largest about the size and proportions of *H. molossus* Thorpe, four more are sufficiently within the range of dimensions of *H. latidens* Thorpe for inclusion in that species. The remaining skulls, all of which are larger than *H. latidens*, compare in size with *H. robustus* and *H. insolens*. Two of the largest skulls, and two incomplete skulls consisting of only the anterior part, which is very large, approach *H. occidentalis* in size.

The problem encountered in trying to identify these specimens as to species is precisely that encountered by Simpson in the *H. oreodontis*, *H. primaevus* and *H. robustus* series. At least six of the specimens, if found isolated, would be referred to Thorpe's

species without question. One of the largest skulls was identified as *H. occidentalis* by Gilmore and exhibited as such. The value of the collection, however, lies in the fact that the specimens were not found one by one in scattered localities but all at the same time and so close together as to leave no doubt of their forming a single assemblage. It is hardly credible that any event could have brought samples of populations comprising four closely related species together in one such limited area. Yet, although certain common cranial characters are evident throughout the group, the differences are equally evident. The skulls differ in size, they differ in proportions, the position of the postorbital constriction is different in some—and there are other cranial variations. The problem lies in the source of these differences. Are they evidence of specific distinction as Thorpe supposed or can they be explained by differences in age and sex? Are these specimens in any way distinct from *Hoplophoneus primaevus*?

In an attempt to answer these questions a study was made of cranial and dental variation in the American cat, *Felis concolor*. The Fish and Wildlife Service of Washington, D. C. has a very fine collection of skulls of this species, arranged regionally and representing all of the described subspecies. Figures and measurements, as well as much valuable data as to the range and habitat are given for them in "The Puma" (Young and Goldman, 1946). Variation in *Hoplophoneus* was compared with variation in the modern species and to test the conclusions arrived at by this method a statistical study similar to that of Simpson was also made. As a result of this study, a detailed discussion of which is presented in this paper, it was concluded that all known specimens of *Hoplophoneus* from the Brule of South Dakota, Wyoming and Colorado are one species, *Hoplophoneus primaevus*. This species undoubtedly covered a much wider area than the territory represented, probably the greater part of western United States, and was divided into a number of subspecies. Two of these can be distinguished with considerable certainty from the material at hand. The one, *Hoplophoneus primaevus primaevus* is represented by the sample used by Simpson, and numerous scattered specimens from South Dakota in various museums throughout the country, the other, *Hoplophoneus primaevus latidens* is represented by Thorpe's types of *H. marshi*, *H. latidens* and *H. molossus* and the nineteen U.S. National Museum specimens previously described. There was probably also a very large subspecies at present known only from the few specimens referred to *H. occidentalis* and perhaps a very small subspecies, a survivor of which is *H. belli* of the Sespé formation of Las Pasos Hills, California.

The work was done under a grant from the Geological Society of America which also provided funds for visiting a number of western museums having important specimens of *Hoplophoneus*. Most of the research, the results of which are presented in this paper was done, however, at the U.S. National Museum, and the writer is deeply indebted to Dr. C. L. Gazin for permission to describe the specimens in the Museum collection and for much personal help with the study. Thanks are due also to Dr. Glenn L. Jepsen for the use of the improtant Princeton collection and Dr. G. G. Simpson for valuable advice and criticism.

VARIATION IN THE PUMA

General Characters

Felis concolor is a well marked species distinguished from other species of *Felis* by a combination of external features, large size, slender form, long tail, short ears and the plain color of the adults. A certain set of cranial characters runs through the entire species. Most typical are the shortness and roundness of the cranium and the moderately convex upper profile of the skull. These are in contrast to the elongate cranium and sagittal concavity of the other large felids. The dentition differs but little from that of the other species of *Felis* but in the shortness of the upper canine and the lack of a pronounced diastema between that tooth and the premolars it is also in contrast with *Panthera*. It is characteristic of the puma, as of felids generally that specific or generic rank is not determined by any one character or set of characters but rather by the combination.

Subspecific Variation

The subspecies of *Felis concolor* are geographic and reflect regional differences in size, weight, color and minor cranial characters. These are maintained rather uniformly throughout ranges of varying area, most quite large but some of very limited extent.

Since the external characters tend to intergrade it is the combination of cranial characters which is largely depended upon to distinguish subspecies. Many of these are not readily measurable. The orbits, for example may be higher or lower in relation to the frontal region. The postorbital process of the frontal and the orbital process of the jugal may be more or less developed, causing greater or less closure of the orbit. The degree of convexity of the upper profile of the skull, the size and configuration of the zygomata, the contact or absence of it of the jugal and the glenoid fossa are also important characters. In fact, all of the cranial characters of the puma are subject to modification and this modification may not be shown by standard measurements. Distinct subspecies may show the same or nearly the same measurements (Young and Goldman, 1946, p. 186).

Cranial differences tend to alter progressively from north to south. There is a tendency also for the same progression in size, the larger subspecies occupying the north and south extremes of the range. Skeletal characters show little alteration and are remarkably uniform throughout.

Subspecies which are widely separated may differ in cranial characters to as great an extent as species, or even genera, such as the puma and the jaguar. For example, a large male no. 26596 from Florida differs decidedly from another male no. 274175 from Colorado. The latter is smaller, the cranium and muzzle are proportionally longer, the postorbital constriction more pronounced, the braincase less inflated, the postorbital processes larger. The cranial differences between the puma and jaguar are of the same type and not much more marked.

Sexual Dimorphism

The skulls of males are in general larger than those of females and sometimes very much larger. The male skull is more angular with a high sagittal crest. The postorbital constriction is narrower and more posteriorly placed. There is little difference in the dentition. The canines are proportionally a little longer in the male.

Males of a smaller subspecies may resemble females of a larger subspecies. For example, a male, no. 231346 from Turas, New Medico, resembles a female from Socorro, New Mexico, no. 249160 in all characters. In fact, the Turas male skull is shorter as to muzzle and cranium, the braincase more rounded, the postorbital constriction less pronounced and more anteriorly placed. Similarly the males of *F. concolor azteca*, a very small subspecies, all resemble females of the large *F. concolor hippolestes*. It follows that while the sexes are readily distinguishable in any population known to be a single subspecies, they cannot be so distinguished if two or more subspecies are intermingled. If, for example, *F. c. hippolestes* and *F. c. azteca* were to be discovered together separating the males from the females on the basis of size would lead to very erroneous results.

The position and size of the postorbital constriction is somewhat more reliable but again cannot be depended upon absolutely if two or more subspecies are involved. Tooth size tends to be correlated in a general way with skull size, the larger skulls having larger sized teeth, smaller skulls, smaller teeth. The canine and carnassial in the male are, however, somewhat larger proportionally to skull size in the male than in the female.

Comparison of Young and Adults

In immature skulls the facial region is always shorter; there is no postorbital constriction of any note; the postorbital processes of the frontal and orbital processes of the jugal are barely showing. Sexual differences are not marked. Young of different subspecies resemble each other more than do adults because the characteristic proportions due to differences in relative growth rates have not yet developed.

In young but mature skulls (permanent dentition in place, but frontal parietal sutures still open) the young of one distinct subspecies show differences from the young

of another. The greater the distinction of the adults, the earlier the appearance of these distinctions in the young.

For example, the adult skulls of *Felis concolor goldmani* (Guatemala) differ markedly from those of *F. c. oregonensis* (Estaconda, Oregon). The cranium is much longer and lower, without the rounded bulge of the North American form. The frontal region is flatter, the nares much higher, the facial region shorter, the canines both upper and lower, larger, the post-canine space more pronounced. The breadth across the postorbital processes is less than the maximum width of the braincase. The postorbital constriction is not sharply marked and forms a gradual curve.

These differences are foreshadowed in the young individuals. No. 80769 (Glendale, Oregon) and no. 248822 (Guatemala) are about the same age. No. 249882 is slightly younger since P^2 is not yet erupted. The muzzle is twice again as long as in the Oregon species and as broad proportionally. The contour of the cranium is lower and less rounded and the postorbital processes more anterior, as they are in the adult. The "waist" is more deeply excavated and more smoothly curving.

The differences become more marked, of course, as the individual grows older. Well marked growth stages can be traced in any subspecies. The full eruption of the canine marks the definitive stage in the development of the facial region and the muzzle. The greatest development of the postorbital constriction is correlated with the full use of the carnassial dentition. These changes appear somewhat earlier in the male than in the female. With age the sagittal crest becomes more pronounced and extends further posteriorly, in large males beyond the condyles. The crests in the female are never as high or as long as in the males, and very old females may have very short sagittal crests. With age the cranial flexure increases, although never exceeding certain limits fixed for the species or subspecies.

In short, the entire contour of the skull can change with age, and unfortunately for ease in distinguishing subspecies or even species, in ways which parallel the distinctions of actually separate groups. Really immature skulls are easy to recognize as such. Mature but young individuals are not so clearly marked, and in comparison with skulls of older individuals may be mistaken for separate species.

CRANIAL AND DENTAL CHARACTERS OF OF THORPE'S SPECIES OF *HOPLOPHONEUS*

The type of *Hoplophoneus marshi* consists of a very incomplete skull without lower jaws or skeletal material. It is an immature individual but the permanent dentition, except the canine, is fully erupted. Thorpe (1920) states that the skull resembles *H. oreodontis* in some respects, *H. primaevus* in others, but has several distinctive features, the most important of which he considers the very large incisor alveoli, the large molar alveoli, the convexity of the upper part of the maxilla and the peculiar shape of the canine. In fact, all of the tooth dimensions are large proportionally to the skull, a juvenile character. The canines are not fully erupted which accounts both for the bulge in the maxillary region and their peculiar shape—straight rather than curved as is usual in *Hoplophoneus*. The posterior portion of the skull is too imperfect to determine precisely the upper profile, but the restoration given by Thorpe is probably correct, in which case, it was horizontal. This again is a juvenile character. There is nothing in this specimen itself which precludes its being, as Simpson suggested, an immature *H. robustus*.

Hoplophoneus latidens is based on a more complete skull with atlas and axis vertebrae. It differs from *H. robustus* and *H. primaevus* primarily in proportions. Thorpe considers it more closely related to *H. robustus*. He sums up the broad differences as: the skull is shorter and broader, has a much lower parietal region; the postorbital constriction is less even than that of *H. primaevus* and much less than that of *H. robustus* while the bimastoid diameter is about equal to that of *H. primaevus* and much less than that of *H. robustus*. He also points to the difference in the shape of the anterior zygomatic pedicle which he thought very significant. This difference consists of a greater relative depth to the jugal below the orbit where it forms the anterior portion of the zygomatic arch.

Thorpe tried to express this configuration in terms of a ratio between the antero-posterior dimension of the anterior zygomatic pedicle and the vertical dimension. Simpson has shown that such an index is highly variable within any one species and not clearly associated with any other features. This is entirely true as regards the index. The difference in the shape of the arch is, however, very real, even though not readily measurable. A similar type of zygoma can be observed in *Hoplophoneus oharrai* and reaches a much more exaggerated development in *Eusmilis*. The arch itself is pressed close to the skull in such a way that the zygoma extends diagonally backward almost in a straight line with the maxillary tooth row. The jugal forms the entire arch meeting the squamosal in sutural contact just lateral of the glenoid fossae with which the zygoma make a sharp angle.

Hoplophoneus molossus is based on an almost complete skull, both mandibular rami, an atlas, an axis and a number of vertebrae. This species Thorpe considered most closely allied to *Hoplophoneus primaevus*. The facial region is broader, the cranium narrower, the postorbital constriction more anteriorly placed as well as smaller in diameter. There is the same difference in the shape of the zygomatic arch between this specimen and *H. primaevus* as between *H. latidens* and *H. robustus*.

In discussing the status of *H. molossus* Simpson points out that while the bone dimensions are small, the tooth dimensions are large. This suggests an immature male, but the specimen in question is not immature. The facial region is proportionally long, agreeing in this with *H. latidens*. The facial-cranial index in *H. primaevus* is 42–55. It is 56 in *H. molossus*, a fact which would not necessarily be important in a larger specimen since this index tends to increase with size, but in so small a skull is possibly significant. The index canine alveolus: prosthion-basion length is also above the observed range of *H. primaevus* and this again is unusual in a small skull. Simpson concludes that the evidence suggests that *H. molossus* is distinct.

Thorpe was primarily interested in comparing *H. latidens* to *H. robustus*, the species he considered nearest to it, and *H. molossus* to its nearest counterpart, *H. primaevus* and devoted little consideration to the relationship between *H. molossus* and *H. latidens*. The two do have a number of significant features in common. They agree in:

1) the configuration of the zygomatic arch.

2) the long facial region.

3) the almost horizontal profile of the skull.

4) the proportionally large size of the dentition.

5) the length of the muzzle and wide diastema between the canine and P^2.

They differ in:

1) the size—*H. latidens* exceeds H. *molossus* in skull length by 22 mm.

2) the length and width of the muzzle, both greater in *H. latidens*.

3) the size of the cranium, which is greater in *H. latidens*.

4) The position of the postorbital constriction, which is more posterior in *H. latidens*.

5) the diameter of the postorbital constriction—less in *H. latidens*.

6) the sagittal crest, which is more strongly marked in *H. latidens* and extends further posteriorly, overhanging the condyles by a considerable margin.

It is possible to interpret the differences as sexual, *H. latidens* being a male and *H. molossus* a female, This would explain the similarity of the former to *H. robustus* and the latter to *H. prinaevus*, a female. If *H. molossus* is reduced to synomony with *H. latidens* it would be possible to consider *H. marshi* a young individual of the same species. This is impossible to determine from the three Yale specimens. It is in this connection that the U.S. National Museum specimens are particularly valuable.

CRANIAL AND DENTAL CHARACTERS OF THE U. S. NATIONAL MUSEUM SPECIMENS OF *HOPLOPHONEUS*

As mentioned in the introduction, six of the skulls in the U.S. National Museum collection made by Pearce in 1942 would be referred to one or another of the species just described. Two of these, no. 18193 and no. 18186 are young individuals. The permanent dentition is in place in both but the sutures

between the squamosal and parietal and the parietal and frontal which close early in life are open. The skulls are small, 130 and 132 mm. respectively. The braincase is proportionally large and rounded, the postorbital constriction but little developed and very anterior in position, especially in 18186. The canine alveoli are unusually large for such small specimens—in fact, the tooth dimensions are all large. The palate is pointed in the manner described by Thorpe for *H. marshi*. In short, except for the slightly smaller size these specimens are *H. marshi* without question.

No. 18187 has approximately the same dimensions as H. *molossus*. The cranial characters are also closely similar. It is noteworthy that this skull although it is about the same size as no. 18186 lacks the juvenile characters of the two previously described. The sutures are closed, the postorbital constriction is more pronounced although still very anterior in position; the mastoid and glenoid pedicles are better developed; the muzzle is longer proportionally and more slender. The tooth dimensions are smaller. It is clearly a mature individual but from the condition of the dentition a young adult. No. 18188 is larger but with the same general characters and more evidence of maturity in the proportions. The muzzle is longer, the sagittal crest strongly developed, the teeth showing more wear. Otherwise the characacters are like those of no. 18187. Both of these specimens are referable to *H. molossus*. Two others are larger than the type but could be referred to that species.

No. 18190, a skull 143 mm. in length is an old individual. The teeth are quite worn, the sagittal crest, although broken in this specimen, was evidently well developed, the mastoid and glenoid pedicles are pronounced. The muzzle is long, the palate narrow, with a constriction just anterior of P^3. There is a wide diastema between this tooth and the canine. The muzzle flares slightly at the canine and is broad anteriorly, with the incisors arranged in a pointed row.

The next specimen in the size series is no. 15925 which repeats the same characters in a more pronounced way. The muzzle is longer, the crest higher, the palatal region narrower proportionally and the flare at the canine greater. The largest specimen is no. 15912 which was exhibited as *H. occidentalis*. Its size is within the range of that species, although this is obscured by the fact that the cranium has been broken from the skull and re-plastered and has suffered considerable distortion, making the posterior part of the skull appear too short for the size of the anterior portion. The sagittal crest is enormously developed, the canine very large, there is a marked cranial flexure (aside from the distortion), the zygomata are very massive, and the lower jaw deep with a pronounced flange.

Seen in a series in this way the common likeness is very apparent. The development of the long facial region and muzzle can be traced through a growth series. The same is true of the upper profile of the skull, which is entirely horizontal in the smaller individuals and becomes somewhat more convex in the larger. The peculiar configuration of the zygomatic arch can be traced through the series becoming more pronounced in the older skulls.

The most marked difference between the skulls, aside from absolute size, is the size and configuration of the postorbital constriction. This is roughly correlated with the size of the skull but is not readily attributable to age. The larger skulls tend to have more deeply excavated and longer "waists," the narrowest part of which is some distance posterior to the postorbital processes. In the smaller specimens the postorbital constriction is notably anterior in position and forms an abrupt notch rather than a gradual curve. These differences are typical of sexual differences in recent felid skulls and suggest the idea that the larger specimens are males, the smaller females.

To summarize: the cranial characters seem to support the hypothesis that the series of skulls just described form a discrete unit of some sort and that the differences which have led to their separation into four species—more, if the criteria used in delimiting these species are valid—are due to age and sexual differences.

RELATION OF THE NATIONAL MUSEUM SPECIMENS TO *HOPLOPHONEUS PRIMAEVUS*

The question of the distinction of the group as a whole from *Hoplophoneus pri-*

maevus is a more difficult one. If the specimens referred to *H. marshi* are compared to the neo-type of *H. oredontis* the minor differences described by Thorpe are readily noted. These differences, however, are not as great as those between *H. marshi* and *H. molossus*. We have seen that this could be explained by the hypothesis that *H. marshi* and *H. oreodontis* are young males of different taxonomic groups, *H. molossus* a female of the same group as *H. marshi*. If *H. molossus* is compared to the skulls which form Leidy's hypodigm of *H. primaevus* this seems a reasonable explanation. The cranial differences are marked. The facial region in *H. molossus* is longer, the upper profile horizontal without the marked cranial flexure of *H. primaevus*, the muzzle longer and more flaring. The incisors have the characteristic pointed arrangement. The zygomata have a different configuration. The tooth dimensions are larger proportionately. These differences, although quite evident and repeated in a number of specimens are not themselves of specific rank. They are of the sort which characterizes subspecies in modern felids.

Large specimens referred to *H. latidens* show even more minor variations. The largest specimens, comparable in size to *H. insolens*, show no difference of importance from many of the skulls referred to that species. Yet the Wyoming skulls seem to form some sort of unit. To determine if this is so, and if it is, what sort of unit seems to require some method of comparison more reliable than simple inspection no matter how careful. This is to be found in the statistical procedures mentioned in the introduction. It was pointed out in the discussion of variation in the puma that subspecies are regional and that certain cranial characters are maintained throughout a given area, but that sexual differences simulate subspecific differences, the females of large species resembling the males of smaller species. Before relying on sexual dimorphism as an explanation of differences it is necessary, therefore, to determine the unity or lack of it of any group and its distinction from another group. In the following statistical analysis an attempt is made to do this for these specimens in so far as that is possible for a small sample.

COMPARISON OF SIZE RANGE AND DISTRIBUTION IN NATIONAL MUSEUM SPECIMENS OF *HOPLOPHONEUS* AND *FELIS C. CALIFORNICA*

Table I gives the figures for 11 continuous variates in 17 of the specimens of *Hoplophoneus*, the cranial and dental characters of which have just been discussed. These were compared with similar measurements for 16 specimens of *Felis concolor californica* as published by Young and Goldman (1946). Table II gives the mean, range, standard deviation and coefficient of variation for the most important of these. The specimens of *Felis c. californica* used in the comparison were collected from the entire range of the subspecies. The area covered includes all of California, except the desert region, and extends into the adjoining portions of Oregon to the north, and the Sierra Juarez and San Pedro mountains to the south. This subspecies rather than any other North American puma was chosen for comparison largely because of the relatively large number of specimens available—some of the subspecies have only five or six—but it is also suitable because the area over which it ranges compares well in size and diversity of topography with that probably occupied by *Hoplophoneus* in the Lower Brule.*

* The White River sediments are generally thought to have been derived from a region of continuous uplift lying west of the present site of the deposits. The finer sediments, which comprise the lower part of the formation are regarded as a deeply weathered subsoil, eroded from the adjacent highlands and deposited in temporary lakes. As the uplift was accelerated erosion predominated over soil formation and the less fine sediments were spread out as sandy river deposits over the clay. The topography of the region, therefore, during the time the specimens of *Hoplophoneus* accumulated and were entombed must have been one of high mountains to the west with broad stretches of alluvial plain at their base. The climate was moist but there is evidence of seasonable rainfall and periods of drought. These conditions are much like those of California today.

It is interesting to note in this connection that the variability of the *Panthera pardus chui* sample studied by Simpson, is greater than that of *Felis concolor californica* even though the former is a "local interbreeding race living under almost uniform conditions" while the California puma is a very widely ranging subspecies living under a great diversity of conditions. Apparently diversity of environment does not necessarily bring about diversity in morphology.

TABLE 1.—MEASUREMENTS (IN MILLIMETERS) OF U. S. NATIONAL MUSEUM SPECI

Variates	18186	18187	18193	15912	18191	18188	18190	18203	15926	18194	18183	18184	15951	18189
Condylo-basal length	130	132	132.3	est. 137	141.5	143.5	148.5	149.4	est. 142.5	156	154	161	162	163
Zygomatic width	—	est. 97.3	104	—	88.5	92	110	126	115			108	—	113
Height of cranium	51	53	54.6	54	58*	50	65.6	—	51			64.6	62.3	54*
Interorbital breadth	43.4	41	42	47	45	41	46	54	—			46.7	57	58
Width over P.O. processes	45.5	—	59	63.5	56	57	61	—	—			59	—	72
Width of P.O. constriction	31	23*	28	25	25.4	29.5	31	31	31			21.5*	29.6	—
Width of palate	68	65	64	65	66.6	62.6	68.5	72	62.5			63	72	70
Length of palate	63	o5	60	—	71	66	71	59.2	70			74	75.6	79.5
Max. tooth row alveolar length	56	61	58	59	58	68	68	—	62.7			71.5	—	70
P^4 crown length	21.4	20	22	21	19	20	23	—	20			21.7	22	22
Upper canine antero-posterior diameter	16	15.7	17	14.3	15	15	15.3	18	15.5			17.4	15	17

* Specimen crushed or distorted.

As will be seen from the tables the ranges studied do not differ significantly in the fossil and Recent groups. The size range measured by the condylo-basal length of the skull, in the *Hoplophoneus* specimens is 130–173 mm. with a standard deviation of 12.6, in *Felis c. californica* the observed range is somewhat less, 161.8–192.5 but the standard deviation is nearly the same, 12.8. The *Hoplophoneus* sample includes young individuals which the *Felis concolor* sample does not. This does not affect the range, however, because one of the adult specimens is as small as the young individuals. The largest specimens of *Hoplophoneus* were omitted also because they were either too incomplete or distorted for accurate measurement. The estimated condylo-basal range of one of these, exhibited as *H. occidentalis* is 180–185 mm. This is well within the possible range of the group, which by any method of estimating it extends to a condylo-basal length of 190 mm. The exact taxonomic position of these specimens and Simpson's "interesting new specimen" which is approximately the same size will be discussed later in the paper in connection with *H. occidentalis*. In any case, even including the larger specimens the standard deviation and variability of the *Hoplophoneus* sample, although more heterogenous as to age compares with that of *Felis concolor californica*.

The variability of the crown length of the carnassial also does not differ significantly, although that of *Hoplophoneus* is somewhat higher. The diameter of the upper canine, on the other hand, strangely enough is more variable in the recent felid than in the fossil specimens. The greatest difference is found in the height of the cranium. The value of V for this dimension is considerably higher in *Hoplophoneus* than in *Felis c. californica*. This is probably due to the effect of distortion in the fossil skulls. The frontal region of the skull is most subject of all to crushing, sometimes very apparent, sometimes not so easily discernible. It is affected both by flattening and lateral compression, neither of which causes much differences in condylo-basal length or dental measurements.

The width of the postorbital constriction is also more variable in *Hoplophoneus* than in *Felis concolor* and this again is probably due, in part, at least, to distortion. This

SPECIMENS OF *H. primaevus latidens* FROM NIOBRARA COUNTY, WYOMING.

18189	15891	18192	18185	15925	16812	18181	Mean	Observed Range	Standard Deviation	V	Number
163	164	165	162	173	—	—	151.7 ±3.05	130–173	12.6 ±2.15	8.3 ±1.42	17
113	—	—	—	119	—	—	—	—	—	—	—
54*	—	63	—	55.6	—	—	56.6 ±1.51	51 –65.6	5.4 ±1.07	9.6 ±1.7	13
58	42	48	43	53	60	59.5	—	41 –58	—	—	—
72	75.8	58.2	68.2	72	80.5	—	—	45.5–80.5	—	—	—
—	18*	26.6	29.2	24	30	—	28.56± .70	24 –31	2.52 ± .49	8.8 ±1.7	13
70	—	—	—	72	73	75.7	67.99±1.1	62.5–72	4.3 ± .78	6.3 ±1.14	15
79.5	—	—	—	80.5	—	—	69.5 ±2.05	60 –80.5	7.1 ±1.44	10.2 ±2.09	12
70	67	68.4	70	70.5	74	74	66.5 ±1.51	56 –71.5	6.06 ±1.04	9.1 ±1.6	16
22	21	—	22	22	21	21.6	21.3 ± .28	19 –23	1.115± .19	5.23± .92	16
17	17.5	18	18	17	18	17.3	16.6 ± .32	14.3–18	1.28 ± .21	7.99±1.3	17

dimension is notably affected by age and sex and for this reason a sample of *Felis c. oregonensis* which included young individuals about the age of the specimens diagnosed as such in the *Hoplophoneus* sample was used. Even so the latter is more variable.

Nevertheless, even the most extreme differences noted are not great enough to warrant the conclusion that the *Hoplophoneus* specimens belong to several species. The correspondence with *F. c. californica* is sufficiently close, in fact, for the hypothesis that the U.S. National Museum specimens comprise, not only one species but one subspecies. If this is the case the differences noted in the description of the cranial characters can only be due to individual variation or sexual dimorphism. The frequency distribution (Table III) of certain of the variates closely connected with sex, such as size, and the width of the postorbital constriction favor the latter idea. Frequency tables of mixed samples of *Felis c. californica* show the same type of bimodality. In other words, in this sample, we are dealing not with three taxonomically distinct units but with one taxonomic unit, composed as in the case of the sample studied by Simpson, of males and females.

TABLE 2—VARIABILITY IN *Felis concolor*, FOR COMPARISON WITH *H. primaevus* DATA IN TABLE 1.

	Mean	Standard deviation	V	No.
	F. concolor californica			
Condylo-basal length	178.5±3.2	12.8 ±2.2	7.1±1.2	16
Upper carnassial crown length	22.4± .25	1.02± .17	4.5± .78	17
Upper canine anteroposterior diameter	13.1± .3	1.2 ± .22	9.1±1.6	17
Height of cranium	72.3±1.46	5.93±1.01	8.2±1.4	17
	F. concolor oregonensis			
Width of P.O. constriction	29.29±.58	2.04±.41	6.6±1.3	12

TABLE 3—FREQUENCY DISTRIBUTIONS. MEASUREMENTS ARE IN MILLIMETERS.

Condylo-basal length			
Hoplophoneus		*F. c. californica*	
130–134	3	160–164	5
135–139	1	165–169	0
140–144	4	170–174	1
145–149	1	175–179	0
150–154	1	180–184	2
155–159	1	185–189	5
160–164	5	190–194	3
165–169	1		
170–174	1		
Width of post-orbital constriction			
Hoplophoneus		*F. c. californica*	
21–21.9	1	26–26.9	2
22–22.9	0	27–27.9	1
23–23.9	2	28–28.9	2
24–24.9	2	29–29.9	0
25–25.9	1	30–30.9	4
26–26.9	0	31–31.9	2
27–27.9	1	32–32.9	0
28–28.9	3	33–33.9	1
30–30.9	1		
31–31.9	4		

COMPARISON OF THE NATIONAL MUSEUM SPECIMENS OF *HOPLOPHONEUS* WITH *H. PRIMAEVUS*

Size Variation

If, in fact, these specimens are one species, with the differences formerly considered of taxonomic value, due to age and sex the question arises whether they are not merely another sample of the *Hoplophoneus primaevus* population studied by Simpson, and differing from it merely as one small sample might be expected to differ from another.

The range in the condylo-basal length in the two groups is almost identical. The means differ slightly. That of the USNM specimens is 151.7, that of the *H. primaevus* group 162.3 but a comparison of the two shows that the difference is not significant.

$$d = 151.7 - 162.3 = 10.6$$

$$\sigma_d = \sqrt{\frac{N_1}{N_2}\sigma_{M_1}{}^2\sigma_{M_2}{}^2}$$

$$= \sqrt{\frac{18}{13} = (3.05)^2 + \frac{13}{18}(4.4)^2} = \sqrt{109.030} = 10.4$$

$$d/\sigma_d = \frac{10.6}{10.4} = 1^+$$

Comparison of the means of the crown length of P^4 in the two groups yields rather different results.

$$d = 21.3 - 19.5 = 1.8$$

$$\sigma_d = \sqrt{\frac{16}{20} \times (1.28)^2 + \frac{20}{16} \times (.30)^2} = \sqrt{2.31} = .48$$

$$d/\sigma_d = 3.7$$

This difference is significant. The same was found to be true of all tooth dimensions and also some other variates, such as facial length.

Proportions and Indices

It was mentioned in a discussion of the cranial characters that the facial region in all of the USNM specimens is long. This is one of the outstanding characters of the group. The facial: cranial index forms one of the best means of measuring this distinction. In *Hoplophoneus primaevus* the range of this index is 42–55. In these specimens it is 50–61. When it is recalled that the condylo-basal range is almost identical in the two groups this difference is significant. Simpson has shown that the facial:cranial index tends to increase with age and size. The smallest specimens of the Wyoming group have an index in the upper brackets of *H. primaevus*. No. 18193 for example and no. 18187, with a condylo-basal length of 132 mm., have a facial:cranial index of 50 and 52 respectively. These are young specimens corresponding to those classified by Simpson as young males (*H. robustus*) with an index of 42. No. 15926 with a condylo-basal length of 142 mm. has a facial:cranial index of 61. Nos. 18190 and 18188 with condylo-basal lengths of 148.5 and 143.5 have an index of 56. If these specimens are included in *H. primaevus* the variability of this index is very much above that of any subspecies of puma and indeed greater than in the species as a whole.

The difference between the prosthion-basion:carnassial index in the two groups is even more significant. That of the Wyoming specimens is 13.2 to 16.6 as a against 7.4 to 14.1 in *H. primaevus*. The cheek teeth are thus definitely larger proportionally. The canine: prosthion-basion index shows less difference, 9.2 to 12.8 in the USNM specimens, 8.5 to 11.1 in the *H. primaevus* series. The small specimens such

TABLE 4—OBSERVED RANGE OF INDICES IN *Hoplophoneus primaevus latidens*.

Indices	18186	18187	18193	15912	18191	18188	18190	15926	18184	15951	18189	15891	18192	18185	15925	16812	Range
Facial length	52	52.5	50	—	51	58.9	60	59	62	67	59.5	67	64.5	60	60	—	50–64.5
Cranial length	94	98	97.5	—	102	97.4	102.4	96	114	119	114	117.4	113.8	117.4	124	—	94–124
Facial: cranial index	55	53	51	—	50	58	58	61	55	56	52	57	57	57	56	—	50–61
Canine alv.: prosthion-basion length	12.3	11.1	12.8	—	10.5	10.4	10.3	10.1	10.9	11.3	10.3	—	10.9	—	9.2	11.5	9.2–12.8
P⁴: prosthion-basion length	15.7	16.6	14.8	—	15	13.9	15	14	13.6	13.5	13.2	—	—	—	13.2	13.4	13.2–16.6
P. O. constr.: prosthion-basin	23.8	17.42	—	—	18.0	20.5	20.9	21.8	—	18.2	—	—	16.1	—	—	19.2	18–23.8

as no. 18193 and no. 18187 have the larger index as would be expected. The index 12.8 and 12.3 respectively for the smaller individuals, however, is above the observed range of those of similar size for the *H. primaevus* group. The index of no. 18187 (*H. molossus*) is 11.1. This is in accord with the diagnosis that this specimen is a female, the other skulls of similar size, young males. (In *Felis concolor* the canines are slightly smaller proportionally in the females than males.)

The postorbital constriction:prosthion-basion relationship also shows a difference which is probably of importance. The range 13.3 to 23.8 is apparently much greater in the Wyoming specimens than in *H. primaevus* but the two smallest figures are from specimens which are compressed laterally and this has probably affected the size of the postorbital contriction although this cannot be positively determined. The principal significance of the difference lies in the fact that the higher figures are found only in the young skulls. The older individuals of the same size or nearly the same size have an index of 17 which is less than that of any of the *H. primaevus* series. No. 18192, with a condylo-basal length of 165 mm. has an index of 16.1 .This skull compares in size with those of the *H. robustus* group where the size is 19.6 to 21.1. There is thus a slight but real difference in the size of the postorbital constriction relative to skull size.

No one of the above indices, nor indeed all of them would prove the distinction between the USNM specimens and *H. primaevus*. Nevertheless they do show that if the former were included in the latter the variability in proportions would be unusual and difficult to explain either as individual variation or sexual dimorphism, in an actually interbreeding population. Taken together with the difference in cranial characters described before and the difference in locality they suggest subspecific distinction, that is, a difference due to partial isolation which has not reached—and possibly will not reach—the level of specific difference. Force is added to this by the fact that the cranial characters have ecological significance.

The USNM specimens are nearer in cranial characters to the earlier species, *Hoplophoneus oharrai* of the Chadron. The

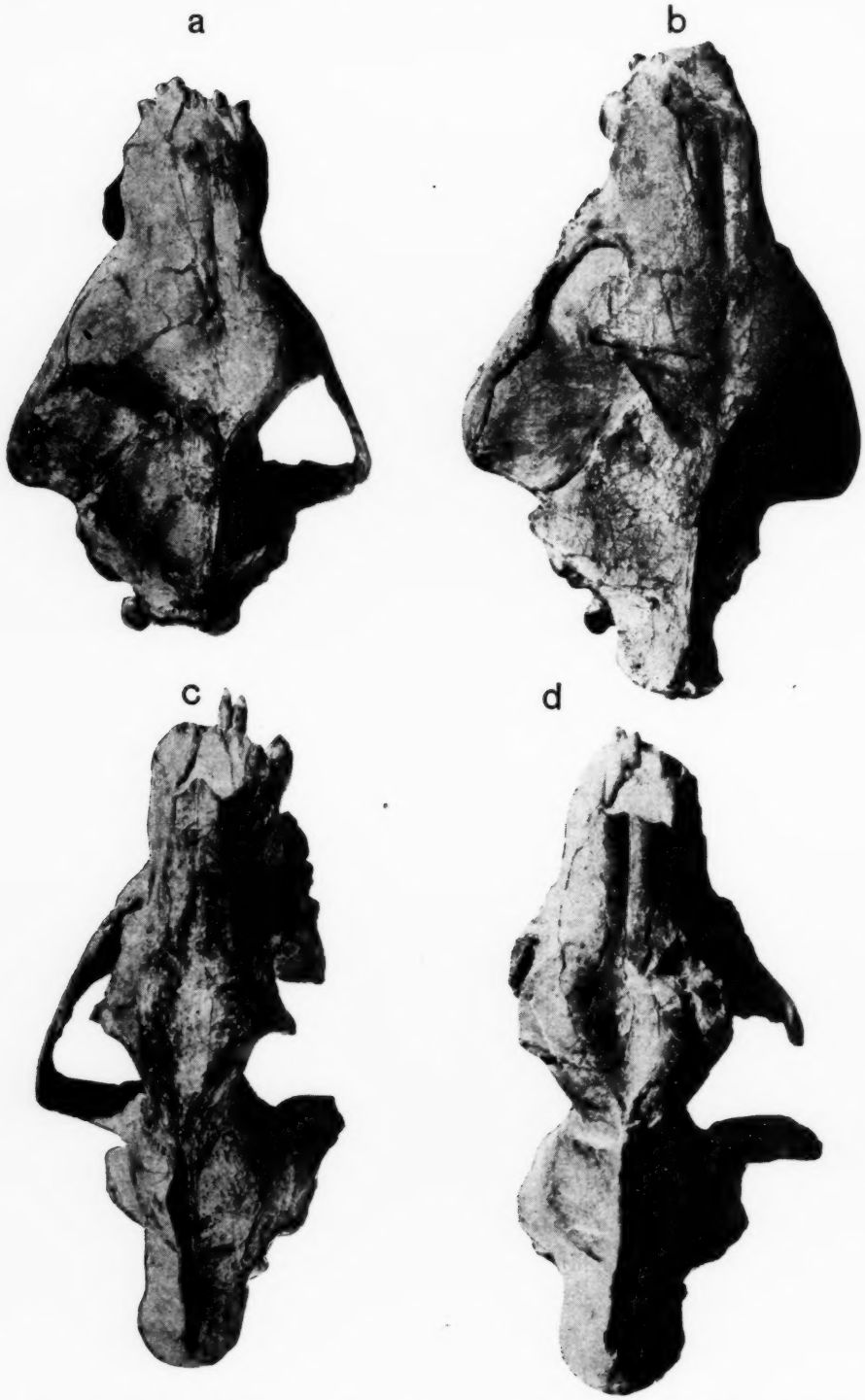

FIG. 1—*Hoplophoneus primaevus latidens* Thorpe, dorsal views of the skull, ×½. *a*, a mature individual, probably female, USNM 18190. *b*, *c*, *d*, mature individuals, probably male, USNM 15925, 18184 and 15951.

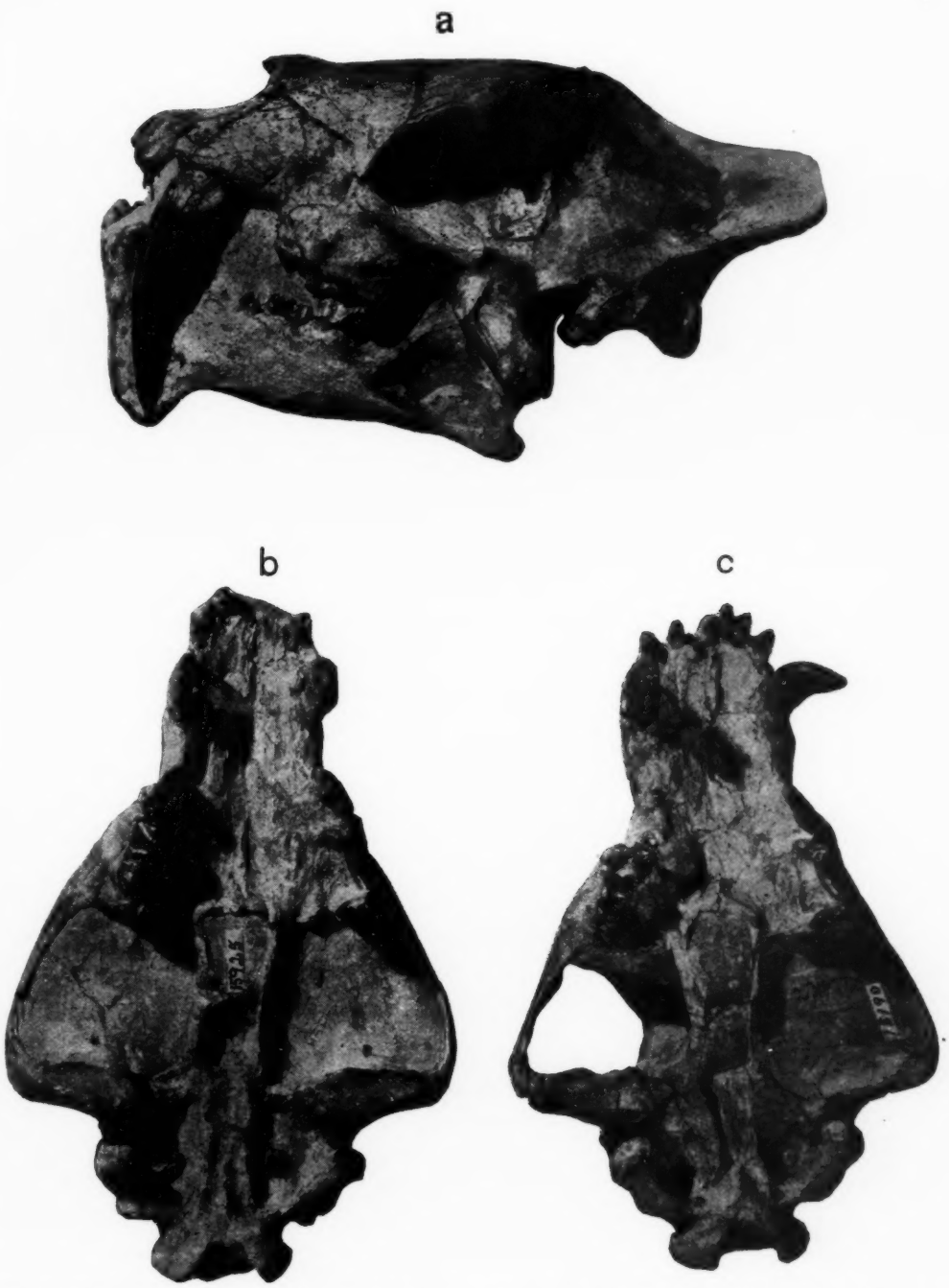

FIG. 2—*Hoplophoneus primaevus latidens* Thorpe, ×½. *a*, side view of skull USNM 15891, formerly referred to *H. occidentalis*. *b*, *c*, ventral views of skulls USNM 15925 and 18190.

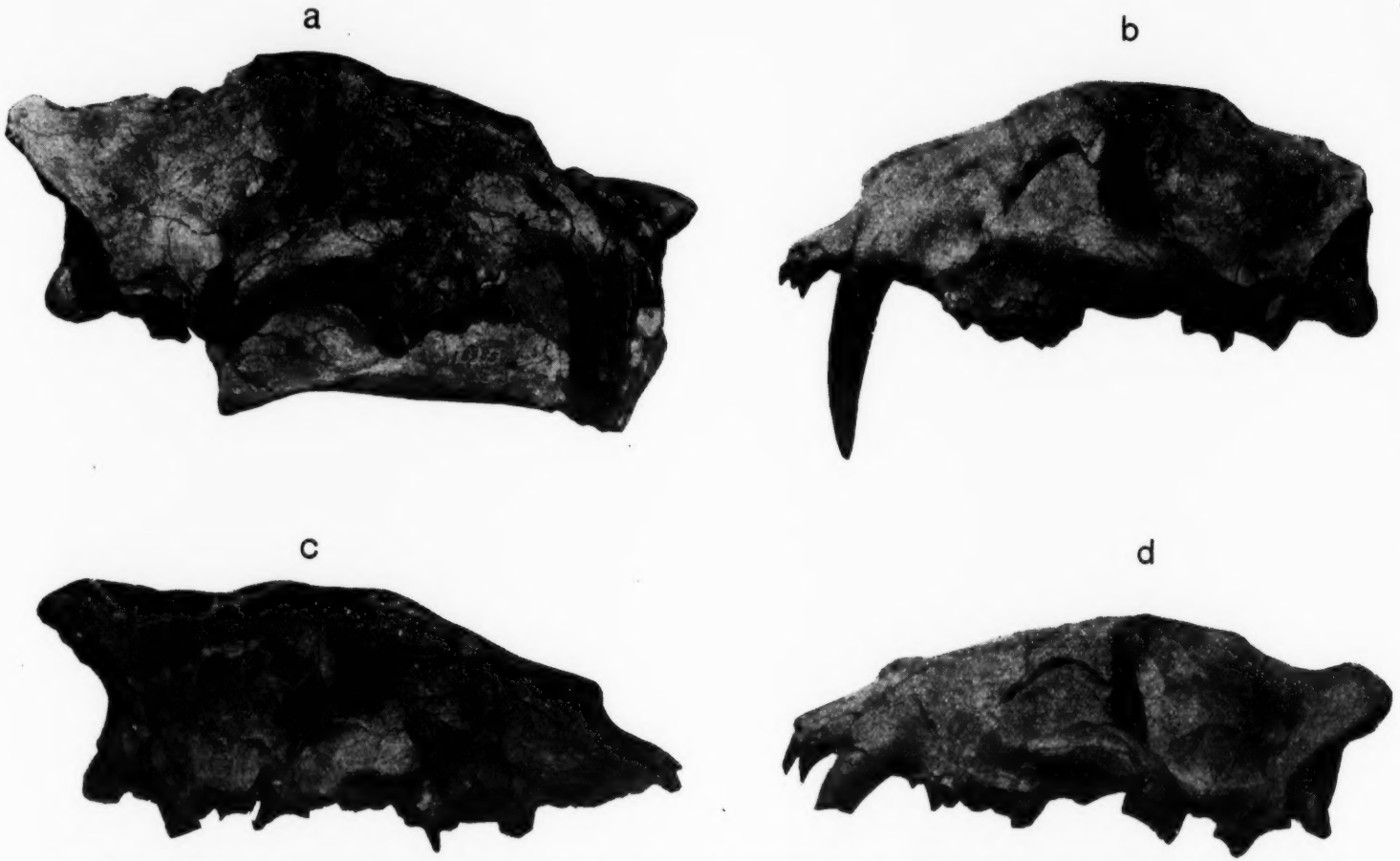

FIG. 3—*Hoplophoneus primaevus latidens* Thorpe, ×½. Side views. *a*, USNM 18185. *b*, USNM 18190. *c*, USNM 15951. *d*, USNM 18188.

long face, horizontal upper profile of the skull, narrow cranium and small diameter of the postorbital constriction, low placed orbits and pointed arrangement of the incisors are all primitive characters, both in the sense of being more like those of the earlier species and in being closer to those of the more generalized carnivores of the period, such as *Daphoenus* and *Pseudocynodictis*. A short face, rounded cranium with marked cranial flexure, high orbits and nares are all typical felid specilizations. *Hoplophoneus primaevus*, although not attaining to anything like the adaptation in this respect of *Felis*, or even of the contemporary *Dinictis* is nevertheless more advanced in these respects than is *H. oharrai*. This suggests that the Wyoming specimens, which resemble *H. oharrai* are, in fact, slightly earlier in time and might be termed a vertical subspecies. On the other hand, the difference may be merely a regional one, with the Wyoming group retaining the more primitive characters. In either case, this distinction could be recognized taxonomically by terming the *Hoplophoneus primaevus* series, *Hoplophoneus primaevus primaevus*, the U. S. National Museum specimens and Thorpe's species, *Hoplophoneus primaevus latidens*. (*H. marshi* has page priority, but since the type of this is an immature specimen. *H. latidens* seems the better name.)

Hoplophoneus occidentalis Leidy

The type of *Hoplophoneus occidentalis* is a lower jaw fragment the distinction of which lies in its size. It lacks the anterior portion, and the coronoid process. A complete mandibular ramus, AMNH no. 1407 was referred to the species by Adams. The depth below the fourth premolar in both specimens is 31 mm. The species is better known, however, from a mounted skull and jaws in the Kansas University Museum. This was first described in a preliminary way by Williston in 1895 and in more detail later in the year by Riggs. In his preliminary description Williston lists the material as consisting of (1) a nearly complete skull and numerous limb bones and (2) the posterior part of a second skull, with mandibles, a part of an upper jaw and a canine.

A recent examination of these specimens with the help of Dr. Robert Wilson of the Kansas Museum shows that, in fact, at least three individuals are involved. The skull and lower jaws as mounted are a composite. The skull, no. 2540, lacks the canine and lower jaw. A canine associated with a fragmentary skull, no. 2651 has been plastered into the alveolus and the tip restored. The canine is recurved and quite unlike that of any specimen of *Hoplophoneus*. The skull to which it may have belonged is very fragmentary and almost unidentifiable. It consists of one occipital condyle, and part of the occiput; the glenoid and mastoid pedicles of both sides broken off from any other part of the skull; the posterior portion of the maxilla and the posterior part of a lower jaw minus the teeth. None of the parts can be measured accurately. The lower jaw is much larger than that of the lower jaw mounted with the skull. It is mounted in such a way that the teeth meet correctly, but this brings the condyles anterior to the glenoid process and the coronoid process almost into the orbit. The canines are obviously disproportionately large for the skull as well as peculiar in shape.

The skeletal material associated with these specimens is very incomplete. That of no. 2540 consists of a number of vertebrae, a complete ulna, tibia and astragalus and calcaneum, the distal two thirds of a humerus and proximal one half of the femur. The astragalus and calcaneum are articulated with each other and with the portion of the tibia. Skeletal bones associated with skull No. 2561 consist of the pelvis which is much broken but articulated to the sacrum, the distal part of the right and left femur, the tibia and a few vertebrae. These parts are much larger than those of No. 2540.

When this specimen was prepared composite mounts and descriptions of the osteology of a species from several individuals were common procedure. The writer is of the opinion that in view of the incompleteness of this early material and the uncertain association too definite conclusions should not be based on it. The skull and jaws as mounted form part of a large permanent exhibit so that they were not available for close study or re-measurement. The skull is incomplete and restored in ways not

exactly ascertainable so that some of the measurements are suspect. The canines certainly do not belong with the skull. They are so unlike those usual for *Hoplophoneus* that there is at least the suggestion that they belong to *Pogonodon*, a specimen of which was found close by. The specimen does show, as do the referred lower jaws that there were large sized hoplophoneids in existence. They were rare, and as Simpson (1941) suggests probably lived in a somewhat different environment than the commoner forms. The proportions, if only the parts certainly belonging to one individual are considered, are not much different from what might be expected in a large individual.

The size does give it distinction. The Standard Range for the *Holophoneus primaevus latidens* population calculated from the sample described in this paper is 82 mm. (for definition of S.R. and the method of calculation see Simpson, 1941a). With 151 mm. as the mean condylo-basal length of *H. p. latidens* the maximum range in length would be 192 mm. The mounted skull, which is not the largest individual of *H. occidentalis* is larger than this. There is a decided hiatus in size between the largest individuals of either the *H. primaevus* or *H. latidens* group and *H. occidentalis*. It may be that the latter is a distinct species.

The cranial characters and proportions of several of the large individuals of the size range 175 mm. to 185 mm. condylo-basal length from South Dakota strongly resemble those of the Wyoming subspecies. This is especially true of Simpson's "interesting new specimen" AMNH No. 38804 and Princeton No. 12590 and 12792, part of Adams hypodigm of *H. insolens*. The facial region is long, the postorbital constriction very marked and the sagittal crest straight with the tip of the inion higher than the plane of the frontal region. The zygomatic arch has the characteristic configuration described for *H. molossus* with a deep anterior portion and a strong curve upward close to the skull.

The characters are not due to size. They are repeated in smaller specimens such as AMNH No. 3901, a recently collected beautiful skull of an old individual and USNM No. 15951 (both of these specimens have a condylo-basal length of about 163 mm.). This specimen, AMNH No. 38804, also has proportionally large canines, as noted by Simpson, with a canine:prosthion-basion index of 12. The index for the larger USNM specimens can only be calculated approximately, but it is about 11.5. This is high for a large individual. (The higher indices are found only in the smaller specimens of the *H. primaevus* series.) Princeton Museum No. 12590 also has a high index, 11.4.

In view of this correspondence in cranial features these specimens probably belong to the *H. primaevus latidens* group. There is another possibility, namely that there was a larger subspecies, not native to either Wyoming or South Dakota, which might include *H. occidentalis*. Without a greater number of complete large sized skulls it is impossible to prove either hypothesis. Specimens are being collected from time to time by various parties especially those from the South Dakota School of Mines. When these are prepared and described our knowledge of subspecific variation in *Hoplophoneus* may be greatly extended.

Some Problematical Specimens

Princeton Museum has a small skull sent to them recently from the South Dakota School of Mines, the measurements of which do not differ appreciably from the *H. oreodontis* specimens diagnosed as small females but which nevertheless has an unusual appearance. This is largely due to the short face, short basicranial region and truncated appearance of the occiput. The

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EXPLANATION OF PLATE 86

All views approximately ×¼. Specimens in the United States National Museum.

Hoplophoneus primaevus latidens Thorpe, dorsal views of the skull. See also plate 87. (p. 554)

FIGS. *1*, *2*—Young individuals, USNM 18193 and 18186.

3—A somewhat older individual, USNM 18187.

4—A mature individual, probably female, USNM 18188.

1

2

3

4

Hough, Subspecies of *Hoplophoneus*

1

2

3

4

Hough, Subspecies of *Hoplophoneus*

skull resembles *H. cerebralis* Cope of the John Day. It is not a young individual.

Simpson has described another very small skull in the American Museum collection which is of unusual appearance. This is a very old individual with characters almost the exact opposite of those of the skull noted above. In many respects these characters are like those of the *H. primaevus latidens* group. The braincase is horizontal, the facial region long and the zygomatic arch and sagittal crest with the typical configuration. The skull is extremely slender and the tooth dimensions small. These latter features are very unlike the Wyoming skulls. The slenderness and narrowness of the palate may be due to lateral compression or perhaps shrinkage during fossilization but the tooth dimensions could not be so affected. The difficulty lies in imagining both of these small skulls to be small females of the same taxonomic group. The American Museum specimen could possibly belong to *H. primaevus latidens* and the Princeton Museum specimen to *H. primaevus primaevus* but such identification in the writer's mind is problematical. Small specimens of unusual appearance are rare as are the larger skull, and with these too, further collecting may show the presence of additional subspecies from other habitats.

REDEFINITION OF THE SPECIES OF *HOPLOPHONEUS*

HOPLOPHONEUS PRIMAEVUS Leidy

(Important synonomy under subspecies)

Type.—USNM No. 99.

Remarks.—In a series of papers Leidy (1851, 1852, 1853) described and figured a much mutilated skull now in the U.S. National Museum as *Machairodus primaevus*. The later definitive description in the Extinct Mammalian Fauna of Dakota and Nebraska (Leidy, 1869) was based on four skulls, one of which is now at Yale, one in the American Museum in New York, and one in the Philadelphia Academy. Marsh had casts made of the Yale specimen, and as Thorpe pointed out (Thorpe, 1920) these are often erroneously thought of as casts of the holotype. They are, in fact, casts of one specimen of the hypodigm of the species as it was described 13 years after the establishment of the name.

Distribution.—Lower Brule of South Dakota, Wyoming, Colorado and Nebraska.

Diagnosis.—Observed size range, that of a lynx to that of a large puma—(130 mm. to 190 mm. condylo-basal length). Upper profile of skull horizontal to moderately convex; diameter of base of upper canine never exceeding the antero-posterior length of the crown of the upper carnassial. M^1 relatively large. Hind limbs longer than the front limbs—index of humerus to femur length 85-87.

HOPLOPHONEUS PRIMAEVUS PRIMAEVUS (Leidy)

Machairodus primaevus LEIDY, Proc. Acad. Nat. Sci. Philadelphia, 1851, p. 329.

Drepanodon primaevus LEIDY, Proc. Acad. Nat. Sci. Philadelphia, (2) 7, pp. 1–472.

Hoplophoneus primaevus COPE, Bull. U. S. Geol. Survey of the Terrs., no. 1, p. 23, 1874.

Machaerodus orecdontis COPE, Synopsis of New Vertebrata of Colorado. Misc. Publ. U. S. Geol. Survey of the Terrs., 1873, p. 9.

Hoplophoneus orecdontis COPE, Ann. Report U. S. Geol. Survey of the Terrs., 1873, p. 509. (Published 1874).

Hoplophoneus robustus ADAMS, Amer. Nat. 30, 1896, p. 49.

Hoplophoneus insolens (in part) ADAMS, Amer. Jour. Sci. (4) I, 1896, p. 429.

Type.—USNM No. 99.

Hypodigm.—Types and principal referred specimens of above species. (See Simpson, 1941, p. 3 for description of sample.)

Distribution.—Lower Brule, South Dakota.

Diagnosis.—Small to moderate size. Observed range of condylo-basal length 135–190. Upper profile of skull moderately

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EXPLANATION OF PLATE 87

All views approximately $\times\frac{1}{2}$. Specimens in the United States National Museum.

Hoplophoneus primaevus latidens Thorpe, ventral views of the skull. See also plate 86. (p. 554)

FIGS. *1*, *2*—Young individuals, USNM 18193, 18186.

3—A mature individual, probably female, USNM 18188.

4—Another individual, less mature than *3*, USNM 18187.

convex, facial region relatively short, facial cranial index 42–55, diameter of canine small in proportion to skull size, index 8.5–11.1. Muzzle short, tapering, diastema between canine and cheek teeth short. Width of cranium relatively great for an Oligocene carnivore.

HOPLOPHONEUS PRIMAEVUS LATIDENS Thorpe
Plates 86, 87, figures 1–3

Hoplophoneus marshi THORPE, Amer. Jour. Sci., 4th ser., vol. 50, Sept. 1920, p. 211.
Hoplophoneus molossus THORPE, ibid., p. 230.
Hoplophoneus latidens THORPE, ibid., p. 214.

Type.—Y.P.M. No. 10050.

Hypodigm.—Y.P. M. Nos. 10049, 10050, 10052, nineteen U.S. National Museum specimens, the catalogue numbers of which are given in Table I, AMNH Nos. 37101, 655, P.M. Nos. 12590, 12792.

Diagnosis.—Small to moderate size, observed condylo-basal range 130–185. Upper profile of skull horizontal, with tip of sagittal crest as high or higher than the highest point of the frontal region: facial region long, facial:cranial index 50–61, tooth dimensions proportionally large, index canine alevolar length: prosthion basion length 9.2–12.8, P^4:prosthion-basion length 13.2–16.6. Postorbital constriction narrow, index of the diameter of the postorbital constriction: prosthion-basion 18–23.8, cranial capacity small.

HOPLOPHONEUS MENTALIS Sinclair

Hoplophoneus mentalis SINCLAIR, Proc. Amer. Phil. Soc., vol. 60, 1921, p. 96.
Hoplophoneus oharrai JEPSEN, Black Hills Engineer, vol. 14, March 1926, p. 1.

Type.—P.M. No. 12515.

Note on synonomy.—The first specimen of *Hoplophoneus* to be described from the Chadron, *H. mentalis*, is based on a lower jaw. In addition two almost complete skeletons are known, the one, described by Jepsen (1926) as *H. oharrai* and now in the museum of the South Dakota School of Mines, the the other an exceptionally fine mount in the University of Colorado Museum at Boulder, Colorado. Only the mandible of these can be compared with the type. It is larger and deeper with a more rounded flange. The differences are almost certainly not enough for specific distinction and it seems necessary to place *H. oharrai* in synonomy with *H. mentalis* and refer the Boulder specimen, as well as a skeleton without a skull P.M. No. 12593, and a fragmentary skull AMNH No. 27798, to that species.

Hypodigm.—S.D.S.M. No. 2417, No. 17456, Univ. of Colo. specimen, P.M. No. 13593, 12515, AMNH No. 27798.

Diagnosis.—Large size, condylo-basal length 185 mm., upper profile of skull horizontal, sagittal crest concave—low anteriorly becoming very high posteriorly where it meets the occipital crest and forms a flaring upturned shield; facial region long, index of face to cranium 57–64; canines large, with a basal diameter equal to or exceeding the crown length of P^4; flange to mandible strongly developed, coronoid process exceptionally truncated. Diameter of postorbital constriction narrow, cranial capacity low. Hind limbs nearly the same length as the fore limbs—index of humerus to femur 94.

Discussion.—The above diagnosis is very tentative. Only two complete skulls are known, one the type, described by Jepsen, and now in the Museum of the South Dakota School of Mines, the other in the University of Colorado Museum at Boulder. There is considerable difference between the two skulls, as a comparison of the measurements will show. The condylo-basal length is the same, but the sagittal crest of the Boulder specimen is higher and shorter. It extends barely to a level with the condyles. The upper profile is less concave. The frontal region of the skull is higher, 75 mm. for the height of the cranium as against 62 mm. in the South Dakota skull; the palate much broader, 166 mm. in contrast to 84 mm. The width across the postorbital processes is also greater. The postorbital constriction has about the same diameter in both, but in the Colorado specimen is much more anteriorly placed. These differences could be interpreted as sexual, the Boulder skull being a female.

Against this interpretation, however, is the fact that the facial region is much longer with a facial:cranial index of 64, and the tooth dimensions are all greater. Since the Boulder skull is almost certainly that of a young individual this is the more

significant. Nevertheless, the differences do not seem sufficient to warrant specific distinction when so few specimens are known. Therefore all known specimens from the Chadron are included in one species which must be *H. mentalis*.

There is also the question of the distinction of this species from *H. primaevus*. There is no feature of the Boulder specimen, except possibly the proportions of the limbs —fore and hind limbs are nearly equal in length—which would exclude it from *H. primaevus latidens*. The characters of the skull and dentition are closely similar to the larger specimens of that group and the limbs are characterized by the same exceptionally heavy muscle attachments. The type, as Simpson points out, differs but little from the large specimens of *H. primaevus primaevus*. It is impossible to settle the matter conclusively without more specimens from the Chadron. A separate species is therefore retained until further evidence can be secured. The writer feels that probably when Chadron hoplophoneids are better known they will fall into one or another of the taxonomic groups of the Brule.

No major diastrophic event separates the Chadron and the Brule in the region where the *Hoplophoneus* specimens are found. The Lower Nodular Layer of the Brule lies with entire conformity on the uppermost Chadron. The hiatus between the two is a depositional one due to the baseleveling of the highlands to the west. As the mountains were worn down and the region reduced to a vast alluvial plain there must have been a mingling of the faunas from different habitats. Eventually this would lead to severe competition and a gradual shift in the adaptive level of the population, but with perfect continuity throughout the process.

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SMALL MAMMALS FROM THE UPPERMOST EOCENE (DUCHESNIAN) NEAR BADWATER, WYOMING

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ABSTRACT—Additions to the upper Eocene fauna of the Wind River Basin in central Wyoming, based on isolated teeth, include an insectivore, doubtfully identified as *Metacodon;* three Paramyid rodents, one probably *Rapamys;* a Sciuravid; a possible Cricetid; an Eomyid; and a rabbit. The dental anatomy of the rabbit is discussed in some detail.

Among other localities visited briefly by the Amherst College paleontological expedition of 1948 was the area along Badwater Creek, in the eastern Wind River Basin of central Wyoming, from which Tourtelot (1946) reported a number of Duchesnian fossils. Due to limited time, only a small collection was made, from the easternmost of Tourtelot's localities, his No. 15 (for the location, see Tourtelot's map). No new large mammals are represented in the Amherst collection, but a number of small mammals can be added to the faunal list. The Carnegie Museum, through Mr. J. LeRoy Kay, very kindly lent me the specimens of *Protadjidaumo petersoni* from the Duchesne River. I wish to acknowledge the financial support received from Amherst College for this expedition, through the Geology and Biology Departments of the College. The preparation of this report was assisted by a grant from the Marsh Fund of the National Academy of Sciences. The cusp terminology used for rodents is that of Wood and Wilson (1936), while that for the lagomorphs is taken from Wood (1940).

In addition to fragmentary specimens of *Protoreodon, Mesagriochoerus, Diplobunops,* a hypertragulid, and *Heteraletes,* the following forms not previously known from this area are represented in the Amherst collections:

Insectivora
  ?*Metacodon* sp.
Rodentia
  Paramyidae
    ?*Rapamys* sp.
    Large Paramyid, indet.
    Smaller Paramyid, indet.
  Sciuravidae
    Sciuravus dubius n. sp.
Cricetidae, indet.
  Eomyidae
    Protadjidaumo sp.
  Small rodent, indet.
Lagomorpha
  Mytonolagus wyomingensis n. sp.

Although these forms are all represented by isolated teeth or portions of teeth, their abundance indicates that there is a considerable microfauna in these beds, which would well repay extensive collection.

?METACODON sp.
Fig. 1

This species is represented by an isolated RM_2, Amherst No. 10019. Initial comparisons were made with the teeth of *Protictops* from the Duchesne River and of *Ictops* from the White River, but the resemblances are much closer to the chadronian *Metacodon.* The trigonid consists of three cusps arranged in an almost equilateral triangle, though the protoconid is the highest of the three and the paraconid is the lowest, whereas the paraconid is higher than the metaconid in *Protictops* (Peterson, 1934, fig. 1). *Ictops* is advanced beyond both *Protictops* and the present form in the reduction of the paraconid. As in *Metacodon magnus,* the talonid consists of a hypoconid and two lingual cusps, one of which is connected with the posterior arm of the hypoconid while the other and larger cusp forms the lingual boundary of the talonid basin. In the arrangement of these cusps, this form is quite distinct from *M. magnus.* Anterior and posterior cingula are present,

at least the former being present in *Metacodon* (Clark, 1937, pl. 256, figs. 1–2; Scott and Jepsen, 1936, pl. 2, figs. 5, 5a). The trigonid is much lower crowned than in *Metacodon magnus*, the height of the protoconid of the present form being only 1.65 mm., as opposed to 2.2 mm. in the Chadron form. Since the talonid has about the same crown height in the two forms, it appears to be much higher in the present specimen. The tooth is 2.20 mm. long, with the maximum width of the trigonid 1.21 mm. and of the talonid 1.27 mm.

This form is unquestionably distinct from *Metacodon magnus*, but the material is not adequate to establish a new species. It seems, however, to be closer to that genus than to any other contemporary insectivores.

?RAPAMYS sp.
Figs. 2–4

An isolated RM_3 (Amherst No. 10014), the talonid of RP_4 or RM_1 (Amherst No. 10029), and a right lower incisor (Amherst No. 10008) are representatives of a single paramyid species which is tentatively referred to *Rapamys*.

In M_3, the metaconid is connected with the anterior face of the protoconid through the anterior cingulum, and the metalophulid II is incomplete, being represented only by a crest extending part way from the protoconid toward the metaconid (Fig. 2). The posterior arm of the protoconid curves around as an ectolophid to the anterior edge of the hypoconid, but there is no suggestion of a mesoconid. The entoconid is connected with the ectolophid through a complete hypolophulid I. The posterior arm of the hypoconid curves around and unites with the posterior cingulum to form a posterolophid.

There is no form with which I am familiar which exactly duplicates the characteristics of this tooth. However, by elimination, it has to be a paramyid. As Wilson has pointed out (1940, p. 76), *Rapamys* of the upper Eocene Sespe deposits of California is the only paramyid in which the entoconid is widely separated from the posterolophid and is directed transversely. Although agreeing in this respect, the present form differs from Wilson's material in the greater development of the hypolophulid, which is incomplete in *R. fricki*. More complete material might show that the Badwater form is generically distinct, but it cannot be demonstrated with the present material, and it is certainly closer to *Rapamys* than to any other described paramyid. There definitely is no particular similarity of the present material to *Prosciurus* (Wilson, 1940, footnote 34, pp. 76–77).

Amherst No. 10029 is the talonid of one of the anterior teeth in the series, obviously belonging to the same form as does Amherst No. 10014. As is normally the case, it is considerably smaller than is M_3. The two specimens agree in all significant structural features, such as the presence of a complete hypolophulid I and the absence of a mesoconid (Fig. 3). Since this is an anterior tooth, the posterolophid is much shorter than in M_3. There is a very large, long root under the talonid.

Referred to this same species is Amherst No. 10008, the right lower incisor of a paramyid, which shows considerable similarity to that of *Rapamys fricki*, although there is by no means identity (Fig. 4). The two sides of the incisor are almost parallel, and the front face is nearly flat, with the enamel extending about a third of the way around onto the lateral face. The enamel is quite thin, showing that this animal did not gnaw very heavy material. The pulp cavity, as seen from the anterior end, is a long, narrow oval. At the root end, it is, of course, much larger, but still retains the same shape.

This tooth must have come from an animal of about the same size as the two cheek teeth, and is referred to the same form because they both appear to resemble *Rapamys fricki* to about the same extent.

PARAMYID indet., Large Size

Another lower incisor, Amherst No. 10001, appears to belong to a paramyid which is quite distinct from that discussed above. The specimen is somewhat crushed, but appears to show a characteristic pattern. The anterior face is widest, and the tooth tapers posterad, being egg-shaped in cross section. The pulp cavity has the same shape as the tooth. The enamel is much thicker than in the tooth referred to *Rapamys*.

PARAMYID indet., Small Size
Fig. 5

Two specimens, Amherst No. 10003, an isolated LM^{1} or ^{2} and No. 10002, the buccal two thirds of an LM^{3}, belong to a considerably smaller paramyid, and apparently represent the same species. The teeth have low crowns and cingula, though these are small on M^{3}. There are some crenulations and surface irregularities, partially eliminated by wear. The conules are well developed, the metaconule in particular being large. In the anterior tooth, the metaconule is connected with the posterior cingulum rather than with the protocone. In M^{3} the metaconule appears to make up the metaloph, as there does not appear to have been any metacone. There does not appear to have been a distinct hypocone on either tooth, though on No. 10003 there is a suggestion of a faint groove separating protocone and hypocone.

SCIURAVUS DUBIUS, Wood, n.sp.
Figs. 6–10

Holotype.—Amherst No. 10020, RM_{3}.

Referred specimens.—Amherst No. 10021, RM_{2}; Nos. 10016; 10017; 10018, which are upper incisors; and No. 10005 which is a lower incisor.

Diagnosis.—Metaconid the highest part of the molars; incomplete metalophulid I; anterior cingulum reaches buccal margin of tooth; small mesoconid present; hypolophulid I incomplete in unworn teeth, becomes complete with wear.

The holotype is an unworn tooth, with the tip of the protocone slightly broken (Fig. 6). The talonid is much narrower than the trigonid. The trigonid is only slightly higher than the talonid, indicating that antero-posterior motion of the jaws in grinding had almost been attained. The mesoconid is very small, appearing only as a slight enlargment of the ectolophid after wear. The hypoconid forms a prominent cusp at the postero-external corner, whose posterior arm continues in a curve along the posterior border of the tooth as a posteroloph, which has a minute expansion which may be called a hypoconulid. The entoconid is small and conical. The basin between the hypolophulid I and the posterolophid is unusually large. A peculiarity is the narrowness of the roots, so that, when seen from below, the tooth overhangs the roots in all directions.

Amherst No. 10021 is either RM_{2} or, somewhat less probably, RM_{1} of a form which also possessed P_{4}. The differences from the holotype are all either due to wear or are of minor significance (Fig. 7). There is a somewhat smaller basin between the hypolophulid I and the posterolophid than in the holotype, which is presumably due to the elongation of the rear of M_{3}. The talonid is slightly wider than the trigonid, the reverse of conditions in M^{3}, but a reasonably normal situation for anterior molars.

Several incisors in the collection (Amherst Nos. 10005; 10016; 10017; 10018) agree with those of sciuravids in the flattened pulp cavity, the extreme transverse flattening of the tooth, and in the limitation of the enamel to the anterior and buccal faces (Figs. 8–10). In addition to being suggestive of sciuravid incisors, these teeth are the commonest small rodent incisors in the collection, which suggests that they belong here since *S. dubius* is the only small rodent represented by cheek teeth. These teeth are very different from those of eomyids, the only other small rodents previously described from the Duchesnian. One specimen, No. 10016, is ten to twenty percent larger than the others in all measurements. Since there is considerable age variation in size of rodent incisors within a single species, all of these teeth are considered to be conspecific.

Sciuravus dubius differs from *Protadjidaumo*, the Duchesnean Eomyid, in the absence of a valley between the metaconid and the anterior cingulum; in the fact that there is a hypolophulid I rather than a hypolophulid II; and in the incompleteness of the metalophulid II. There are suggestive similarities of this form to the middle Eocene *Reithroparamys*, but the latter does not show the complete hypolophulid I. It does, however, possess a pattern which could have served as the starting point for the evolution to *S. dubius*. The closest similarities of the Badwater species appear to be with *Sciuravus*, which has already been described from the Uinta, although better material would probably require reference to a new genus.

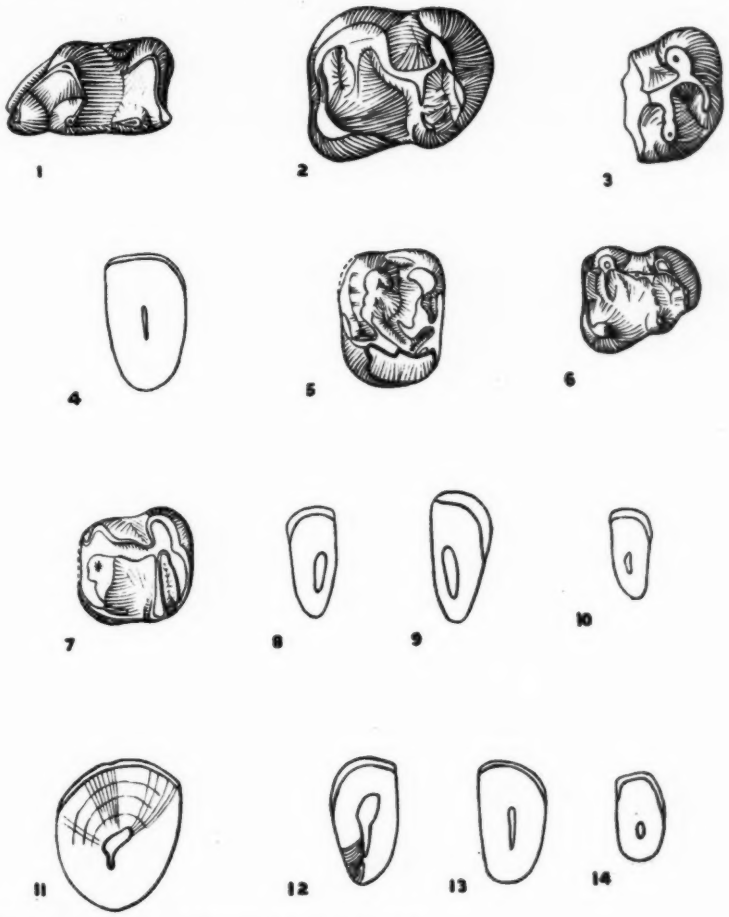


FIG. *1*—*?Metacodon* sp., RM_2, Amherst No. 10019. ×10.
2—*?Rapamys* sp., RM_3, Amherst No. 10014, ×5.
3—*?Rapamys* sp., talonid of RP_4 or RM_1, Amherst No. 10029, ×5.
4—*?Rapamys* sp., cross section of RI_1, Amherst No. 10008, ×5.
5—Paramyid indet., LM^1 or LM^2, Amherst No. 10003, ×5.
6–10—*Sciuravus dubius* Wood, n. sp. *6*, Holotype, RM_3, Amherst No. 10020, ×10.
7—RM_2, Amherst No. 10021, ×10.
8—Cross section of LI^1, Amherst No. 10017, ×10. Viewed from rear.
9—Cross section of LI^1, Amherst No. 10016, ×10. Viewed from front.
10—Cross section of RI_1, Amherst No. 10005, ×10.
11—Cricetid indet., cross section of LI^1, Amherst No. 10004, ×10.
12—*?Protadjidaumo* sp., cross section of RI^1, Amherst No. 10038a, ×10.
13—*?Protadjidaumo* sp., cross section of LI_1, Amherst No. 10038b, ×10.
14—Rodent indet., cross section of RI_1, Amherst No. 10038c, ×10.

CRICETID indet.
Fig. 11

A fragment of a left upper incisor, Amherst No. 10004, is tentatively referred to this family. The tooth is much more nearly circular in cross section than are the teeth of any other rodents in the collection, and very clearly shows both radiating dentine tubules and a series of concentric rings surrounding the angulate pulp cavity. The enamel is limited to the anterior face of the tooth, and there is a very slight groove

near the middle of the enamel. In its approach toward equality of antero-posterior and transverse diameters and in the bending of the pulp cavity in cross section, this form is very suggestive of at least some specimens of the middle Oligocene *Eumys*, and is quite different from all other forms with which it has been compared. Therefore, in spite of the fact that no cricetids have heretofore been reported from so early a date, this specimen is tentatively referred to the Cricetidae.

Table 1—Measurements of Rodent Cheek Teeth
(all measurements in mm.)

	Antero-posterior	Width trigonid	Width talonid
?Rapamys sp., Amherst No. 10029 P_4 or M_1			3.52
?Rapamys sp., Amherst No. 10014 M_3	4.95	4.08	3.75
Paramyid indet., small, Amherst No, 10003 LM^1 or ^{2}	2.80	3.47	3.54
Paramyid indet., small, Amherst No. 10002 LM^3	2.90		
Sciuravus dubius, Amherst No. 10021 RM_2	1.52	1.35	1.48
Sciuravus dubius, Amherst No. 10020 holotype, RM_3	1.56	1.39	1.15

Table 2—Measurements of Rodent Incisors
(all measurements in mm.)

	Width of Incisor	Antero-Posterior	Thickness of Enamel
?Rapamys sp., Amherst No. 10008 RI_1	2.14	3.59	0.11
Paramyid Indet., large, Amherst No. 10001	2.34	4.52	0.19
Sciuravus dubius, Amherst No. 10005 RI_1	0.54	1.18	0.12
Sciuravus dubius, Amherst No. 10016 LI^1	0.83	1.72	0.17
Sciuravus dubius, Amherst No. 10017 LI^1	0.65	1.45	0.13
Sciuravus dubius, Amherst No. 10018 RI^1	0.72	1.47	0.13
Cricetid Indet., Amherst No. 10004 LI^1	1.65	1.99	0.16
?Protadjidaumo sp., Amherst No. 10038a RI^1	0.90	1.66	0.11
?Protadjidaumo sp., Amherst No. 10038b LI_1	0.89	1.60	0.08
Rodent Indet., Amherst No. 10038a RI^1	0.63	1.16	0.07

?Protadjidaumo sp.
Figs. 12–13

A small rodent is represented in the collections by a right upper (Amherst No. 10038a) and a left lower incisor (No. 10038b). These are of about the same size, have enamel of about the same thickness, and both have essentially the same type of rounded anterior faces, and are considered conspecific. There is a striking difference in the shapes of the pulp cavities, however, that of the lower tooth being very narrow as in the incisor referred to *Rapamys*, and that of the upper being more ovate. Unfortunately, the lower incisor is not preserved in the holotype of *Protadjidaumo petersoni*. In a referred specimen (Carn. Mus. No. 9949), a lower jaw with no cheek teeth, the incisor is preserved and is almost identical with Amherst No. 10038b. The upper incisor, No. 10038a, is suggestive of the upper incisors of a specimen of *Paradjidaumo minor* (A.E.W. No. 9111) from Pipestone Springs. Therefore, these specimens are tentatively referred to *Protadjidaumo*.

Rodent indet.
Fig. 14

A small rodent is represented by a portion of a single incisor, Amherst No. 10038c. This tooth is about the size of the lower incisor referred to *Sciuravus dubius*, but it is entirely different from that form in shape, being more uniformly rounded. Moreover, it has thinner enamel, a rounder pulp cavity, and a flat anterior face, with the suggestion of a faint sulcus. In addition, the enamel extends onto the median side, and covers about half of the lateral face.

This small collection of rodents, then, indicates the presence of two large paramyids, one referred to the genus *Rapamys;* a smaller paramyid; a sciuravid, *Sciuravus dubius;* a form questionably referred to the Cricetidae; an eomyid, perhaps *Protadji-*

daumo; and a small rodent of uncertain relationships; and suggests that future collecting in this area would be very productive of significant rodent material.

MYTONOLAGUS WYOMINGENSIS
Wood, n.sp.
Figs. 15–24

Holotype.—Amherst No. 10022, an isolated RP^3.

Referred specimens.—Amherst Nos. 10023–10028; and 10033–10037, including representatives of most of the teeth.

Diagnosis.—Low crowned with well developed buccal roots in upper teeth; poorly developed hypocone and weak hypostria on P^{3-4}; enamel reduced on external side of upper teeth and anterior side of lowers, and lost after wear; little or no cement on teeth.

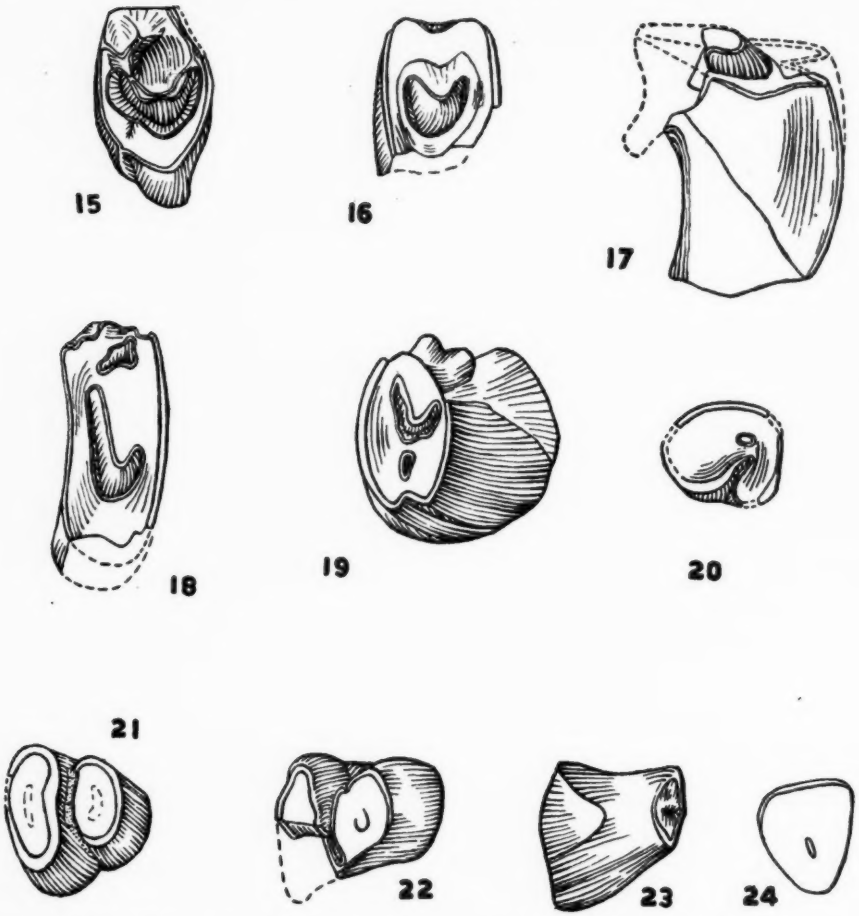
This rabbit is much the most abundant of the small mammals from the Badwater locality, being represented by thirteen specimens, all isolated teeth. Up to now, while *Mytonolagus* has been reported from the Duchesne River (Peterson, 1934, p. 374; Burke, 1943a, p. 400; Scott, 1945, p. 220), no description of them has been given, Burke merely stating that they "are fragmentary, but are referred to the same genus as the Myton fossils," while the other authors merely cite Burke.

This species is closest to *Mytonolagus petersoni* in its general characteristics, but is distinctly more advanced, especially in the considerably greater areas in which the enamel was never deposited. However, in some details of the premolar, *M. wyomingensis* may be more primitive than *M. petersoni.* Since, in most respects, *M. wyomingensis* is much more primitive than *Palaeolagus,* it is considered an advanced species of *Mytonolagus,* although it is not identical or nearly identical with the Uinta form, but is merely toward the *Mytonolagus* end of a presumable *Mytonolagus-Palaeolagus* continuum. At present, it seems probable that *M. wyomingensis* is not descended from *M. petersoni.*

The holotype, Amherst No. 10022, is almost completely unworn, and shows the elements of the pattern better than does any other tooth (Fig. 15). The root end of the tooth, unfortunately, is broken off. It does not agree exactly with any of Burke's material (1934a, pl. L), but it is closest in conformation to his figures of P^3. The extreme shallowness of the hypostria, and the way the hypocone appears as an afterthought, as well as the approximately quadrate shape of the tooth, show it to be a premolar, and the short anteroloph suggest that it is P^3. However, the anteroloph unites buccally with the paracone, which is a very progressive character for a tooth so little worn. The crescentic valley seems shorter than in *Mytonolagus petersoni* (Burke, 1934a, pl. L, Fig. 5). The transverse narrowness of the posterior side of the tooth in *M. wyomingensis* is in accord with what one would expect in a more primitive stage if Wood's phylogeny of leporid premolars is correct (Wood, 1940, fig. 114). The metacone arises from the metastyle on the posterior margin, about a third of the distance in from the buccal face. This character and the poor development of the hypocone seem more primitive than in *M. petersoni.* At the buccal margin of the crown, the metastyle crest is poorly marked, but forms the buccal wall of most of the tooth, and is separated from the posterior wall of the crown by a faint depression. The buccal valley is nearly closed off by the metastyle crest.

The lingual half or two-thirds of another P^3, Amherst No. 10023, is one of the most hypsodont upper teeth in the collection, the lingual root being very long with the enamel extending nearly to its base. A buccal root is present beneath the antero-external corner, but it is impossible to tell whether or not a posterior root was present. Burke (1934a, p. 403) reports only a single buccal root in P^3 of *M. petersoni.* The anteroloph is not as pronounced as in the holotype, since it does not extend over to the buccal roots, but is entirely supported by the long lingual root. The hypostria is visible at the occlusal surface, but rapidly fades toward the roots.

A tooth interpreted as RP^4 (Amherst No. 10026) is quite different in shape from any of the other teeth in the collection, being greatly elongate transversely. This is due to the angle of wear, and does not indicate any actual greater diameter than in the other teeth (Fig. 18). The buccal roots are very large, and, due in part to the angle of



FIGS. *15–24*—*Mytonolagus wyomingensis* Wood, n. sp. *15*—Holotype, RP^3, Amherst No. 10022, anterior end of tooth to right.
16—RM^1, Amherst No. 10024. Anterior end of tooth to right.
17—RM^1, Amherst No. 10025. Posterior side of tooth showing end of enamel on root.
18—RP^4, Amherst No. 10026. Anterior end of tooth to right.
19—LM^2, Amherst No. 10027.
20—LP_3, Amherst No. 10028.
21—LP_4, Amherst No. 10033.
22—RM_1, Amherst No. 10034.
23—Trigonid of LM_1 or $_2$, Amherst No. 10035. Oblique view to show interruption of enamel on anterior face.
24—Cross section of LI_1, Amherst No. 10036.
All figures ×7.5.

wear, extend well under the crown of the tooth, while the buccal margin of the tooth overhangs the roots. There are two buccal roots, differing from *M. petersoni* where there is only one (Burke, 1934a, p. 404). Burke has suggested that the presence of a single root in *M. petersoni* is a specialization from a condition with two roots. The enamel extends only a short distance down the anterior and posterior faces of the tooth, except on the lingual root where it extends as far down as the specimen is preserved. The crescentic valley rests above the space between the buccal and lingual roots, but

its lingual tip extends down into the lingual root. The lingual margin of the tooth is missing. The posterior arm of the crescentic valley is twice as long as the anterior, and the metacone is clearly shown as a cusp rising well above the general level of the tooth. At the buccal margin of the tooth, there is a prominent lake, formed by the union of the anteroloph and the metastyle.

Amherst No. 10024, probably RM^1, is broken, but the buccal two-thirds of the tooth is preserved (Fig. 16). The enamel was interrupted at both ends of the buccal margin of the crown although it is still present as a patch at the center of the buccal margin and the crescentic valley is still preserved. In the interruption of the enamel at such an early stage of wear, it is much more advanced than is *M. petersoni*.

An anterior molar (probably RM^1) is represented by Amherst No. 10025, of which most of the anterior half is missing. The broken surface of this specimen clearly shows, as does M^2 of *M. petersoni* (Burke, 1934a, pl. L, fig. 1), that in the molars, the hypostria and the crescentic valley are lost through wear at about the same time, so that teeth which do not have the hypostria but which still retain a large crescentic valley must be premolars. There is a distinct groove along the posterior side of the tooth opposite the lingual side of the crescent. The enamel extends to the base of the tooth on the lingual side, and the lower limit of the enamel forms an angle of about 45° with the axis of the lingual root (Fig. 17).

In Amherst No. 10027, probably LM^2, the anterior arm of the crescentic valley is slightly longer than the posterior, the metacone is worn down level with the rest of the crown, and no traces of pattern are present along the buccal margin (Fig. 19). A lake is present on the lingual half of the crown, marking the isolated buccal end of the hypostria, the lingual part of which remains as a shallow groove. This tooth is therefore in the same condition of wear as Russell's specimen from the Swift Current of Saskatchewan (Russell and Wickenden, 1933). There is no enamel around the buccal margin of the tooth, which was largely due to non-deposition, although there may have been slight breakage. On the lingual side, enamel extends to the tip of the root. The two buccal roots are large. The posterior side of the tooth is concave and the anterior side is convex.

A single anterior lower premolar is present, Amherst No. 10028, a badly worn LP_3. It is, however, not as badly worn as that of *M. petersoni* (Burke, 1934a, pl. L, fig. 3), since there is a small remnant of a valley linguad of the central valley (Fig. 20). The posterior portion, as in *M. petersoni*, is antero-posteriorly compressed, and there is also no internal fold. There is a differentiation in the thickness of the enamel at various portions of the crown, as an initial step toward its interruption. The crown height is greatly reduced, which may in part be due to wear, and the two roots are partially divided, as is also true of *M. petersoni* (Burke, 1934a, p. 410).

An anterior lower tooth (Amherst No. 10033, probably LP_4, Fig. 21) is badly worn and shows relatively little. It indicates, however, that the union of the trigonid and talonid comes quite late in life, the lingual fold being persistent as in *M. petersoni* (Burke, 1934a p. 413). Cement is present, though in small quantities and limited to the space between the trigonid and talonid, The enamel on the anterior face of the talonid is exceedingly thin, and that on the anterior face of the trigonid is somewhat thinned. The roots are very large and well developed, but are partly fused.

The first lower molar (Amherst No. 10034) is about the same size as P_4. In the stage of wear represented, the two moieties have united at the buccal margin, there being no trace of a buccal fold, and the buccal half of the talonid is very closely appressed to the trigonid (Fig. 22). The space between the two contains cement, which is limited to the narrow valley. On the anterobuccal face of the talonid there is a faint furrow, which extends well down toward the base of the crown. This is not duplicated in any of the Oligocene leporids with which I am familiar, though it is suggested in some specimens of M_1 of *Megalagus brachyodon* (Wood, 1940, figs. 108–109), where it does not extend as far down the crown. This is presumably a remnant of the ancestral pattern of the talonid. No indications of such a fold are given by Burke for *Mytonolagus petersoni*. Perhaps this furrow is

retained longer in *M. wyomingensis* as the talonid is not as much basined with wear as in other leporids. This tooth has already reached a stage of development where the enamel is interrupted part way up the anterior face.

Amherst No. 10035 is the trigonid of a completely unworn molar, with the crown pattern, as far as it goes, still preserved. The anterior face is convex, with a faint depression toward the buccal margin which would result, with wear, in producing the pointed buccal margin seen in *M. petersoni* posterior marginal arms surrounding a trigonid basin which is very shallow except for a deep pit just in front of the posterior angle of the trigonid. Various minor irregularities are present on the surface of the trigonid basin, but it does not seem possible to correlate these with the underlying pattern. Since the significant differences between M_1 and M_2 are in the talonid, it is not possible to identify this tooth precisely.

Only a single fragment of an incisor is preserved in this collection which could be

TABLE 3—MEASUREMENTS OF TEETH OF *Mytonolagus*
(all measurements in mm.)

	Antero-posterior	Anterior Width	Posterior Width
RP^3, Amherst No. 10022	2.08	2.92	2.92
RP^4, Amherst No. 10026	1.71	ca. 4.25	ca. 4.20
RM^1, Amherst No. 10024	2.07		
RM^1, Amherst No. 10025			3.14
LM^2, Amherst No. 10027	1.71	2.71	2.42
LP_3, Amherst No. 10028	2.14	1.63	1.83
LP_4, Amherst No. 10033	2.07	2.16	1.59
RM_1, Amherst No. 10034	2.08		1.94*

* Measurement at wear surface. Lower down the tooth narrows to 1.54.

(Burke, 1934a, pl. L, fig. 11). At the buccal margin, the enamel extends to the base of the tooth; at the lingual margin, nearly to the base; but in the center of the anterior face, it does not reach as far as halfway down (Fig. 23). The posterior face of the trigonid is concave, and is entirely separate from the talonid nearly to the base of the tooth. The union between trigonid and talonid would begin at the buccal margin of the tooth, and spread gradually linguad with further wear. A small lake might be formed for a brief period. The crown has a complete cap of enamel, but it is very thin except around the edges of the crown. In fact, it is almost transparent, but it can be detected in the proper light. This tooth differs from the teeth of *Megalagus brachyodon* (Wood, 1940, fig. 108) and of *Palaeolagus temnodon* (op. cit., figs. 83–84) in the complete absence of cement over the crown, thus permitting a clearer view of the pattern. As in *P. temnodon*, (op. cit., p. 302), there is no accessory cusp near the protoconid, the pattern apparently being merely protoconid and metaconid, with anterior and

referred to *Mytonolagus wyomingensis*. This specimen, Amherst No. 10036, is a left lower incisor. It has a more rounded antero-buccal corner and a more curved lingual margin than in the rabbits from Pipestone Springs, but these are minor differences, and the tooth is unquestionably that of a lagomorph (fig. 24).

	No. 10036
Antero-posterior	1.93
Transverse	1.71
Thickness of Enamel	0.13

This material indicates a rabbit which was anything but a primitive lagomorph, in that but little remained of the basic cusp pattern and all the leporid characters seem already to have developed. For a rabbit, however, it is primitive in:

(1) the near absence of cement;
(2) the relatively low crowns;
(3) the strong buccal roots; and
(4) the persistent traces of an original cusp pattern.

All of these characters separate *Mytonolagus*

wyomingensis clearly from *Palaeolagus temnodon* and *Megalagus brachyodon* of Pipestone Springs, and indicate a form close to, and perhaps even more primitive than, the Uinta *Mytonolagus petersoni*.

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STEREOPHOTOGRAPHY AS A TOOL OF THE PALEONTOLOGIST

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INTRODUCTION

THROUGH the years gradual improvements in photographic techniques have contributed greatly to the field of scientific illustration, so that today it is feasible for the average worker in paleontology to accompany his descriptions with faithful illustrations. Nevertheless, the question might be raised: Are all available techniques being used to produce the best possible photographic results?

Stereophotography, or the taking of photographs suitable for three-dimensional vision, is a simple process based on elementary visual and optical principles. In the opinion of the writer, its wider use would greatly increase the value and usability of published illustrations and would prove particularly advantageous for record and reference files and as a teaching aid.

Sequences of aerial photographs of terrain which can be studied stereoscopically are already familiar to most geologists. Stereograms extracted from such photographic series have appeared lately as illustrations in several geologic texts and in at least one journal. A discussion of the value of stereophotography for picturing lateral views of terrain or geologic outcrops is not within the scope of the present paper. It may be noted, however, that its merits in this respect are undergoing the scrutiny of several experimenters.

Although the use of stereophotography for paleontologic illustration has been suggested on several occasions, its actual application has been very limited. One of its first advocates was George H. Hudson. In a paper entitled "The Use of the Stereogram in Paleobiology" (Hudson, 1913) he presented thirteen plates, each a single stereogram of a stelleroid eleutherozoan, arranged to be viewed with a modified parlor stereopticon. In a second paper (Hudson, 1925) he further demonstrated the advantages of illustrations in three dimensions by comparing a stereogram and a drawing of the same portion of the surface of a stelleroid, pointing out both the greater accuracy and the greater detail inherent in the former. Schmidt (1948) suggests the application of the principles of stereophotography to radiography and presents, among other illustrations in her plates, three stereograms of radiographs showing internal structures of brachiopods.

In American geologic literature three examples of the employment of stereophotography simply as a vehicle for paleontologic illustration and completely divorced from any propagandist approach can be cited. The earliest of these is the treatise on American Mesozoic mammals by G. G. Simpson (1929) in which appear 59 stereograms of mammalian teeth. The second is a volume comprising four papers on conodonts by Branson, Mehl, and Branson (1933) and containing a total of 644 stereograms and 181 conventional photos arranged in 38 plates. The third example is a paper by H. J. Sawin (1947) illustrated with one figure of of four stereograms of small reptilian bones, in addition to other figures of conventional photographs.

EQUIPMENT

The techniques involved in producing extremely satisfactory stereograms can be mastered easily. The necessary photographic equipment is of sufficiently simple design as to be available at low cost to any individual or organization with moderate mechanical facilities, or more expensive and elaborate equipment may be obtained from manufacturers of optical and photographic instruments.

An existing camera can be used to take stereoscopic views by so modifying the camera mount that two pictures can be taken of the same object from slightly different angles. Branson, Mehl and Branson (1933, p. 17) suggest several ways in which

this may be done. A design for a simple stereoscopic camera which, with adaptations to fit individual needs, should prove of universal service to the paleontologist is presented by Gott (1945) along with a discussion of some of the more technical aspects of the subject.

The angle between the two lines from object to image in the two camera positions determines the apparent relief seen in the resulting stereogram. A stereogram employing a small angle (less than 5 or 6 degrees) appears to possess less relief than natural. On the other hand an angle of 10 or 11 degrees or more produces an exaggerated relief which accentuates the third dimension (conceivably desirable in certain instances) but does so at the expense of accuracy. A more generally satisfactory range seems to lie between these limits.

The optical instrument necessary for the close examination of stereophotographs is a small stereoscope, such as the collapsible pocket type with 2- or 3-power magnifying eyepieces widely used in wartime and since for the study of aerial photographs. A simple "home-made" device on the same principle will serve equally as well. However, for casual inspection no special instrument is necessary. With a little practice it is possible for one to fuse the two images of a stereogram by merely looking at them with the unaided eyes, providing only that the images are not too widely separated.

STEREO- VERSUS CONVENTIONAL PHOTOGRAPHY

In current times when economy in the number of plates is a factor of prime importance in the illustration of an article, the wide use of stereophotography for this purpose has the significant drawback that considerably more plate space is required than for conventional photographs. Not only are two photographs needed for each view, but they must be spaced a given distance apart. However, as will be outlined below, the extra space needed can be kept at a minimum by a little careful planning and arrangement. The obtainable results are so superior to ordinary photographs that careful consideration of the pros and cons of the case seems warranted.

First, let us consider for what purposes and for what types of fossils stereophotography would or would not be particularly advantageous. Since its whole purpose is the presentation of three-dimensional views, it obviously would not be appropriate for illustrating items with only two prominent dimensions, i.e. specimens which are either originally flat, secondarily flattened, or which are illustrated by photographs of thin or polished sections. Neither would it be satisfactory for the illustration of specimens the lateral dimensions of whose photographic images are in excess of 2½ to 3 inches. This is the limitation imposed by the spacing of the two elements of a stereogram. Nor would it be practicable where extensive retouching is generally the practice following extremely high magnification, since it would be most difficult to retouch two different photos of the same specimen in an identical manner.

The main forte of stereophotography, then, would be in the illustration of moderately small specimens with prominent three-dimensional form. It would have particular advantage over conventional photography for illustrating structural details hidden in concavities where profile views cannot be obtained, but its merit would be considerable in figuring any specimens whose surface exhibits the third dimension to such an extent that foreshortening of some feature takes place regardless of the direction of the view. Stereophotography, though not entirely obviating the necessity for views from other directions, would offer in one glimpse an over-all picture of three-dimensional form which ordinarily could be comprehended only after careful study and comparison of several views taken from different angles by conventional photographic methods. The illustrations in Simpson's paper (1929) are excellent examples of this. Here crown views of teeth by themselves reveal little of their true shape if the photographs are examined in the normal manner, but viewed stereoscopically the conformation of the surfaces immediately becomes clear.

Stereo-illustration would seem particularly effective for entire uncrushed specimens of the following: Foraminifera, sponge spicules, small corals, conodonts, blastoids, cystoids, small crinoids and echinoids, brachiopods (particularly interiors and

hinge structures), small molluscs, ostracodes and trilobites; or, for details of portions of the surface or structure of any strongly three-dimensional item, including small vertebrate bones or teeth.

The normal photographic process as it involves time and materials is complicated by stereophotography only to the extent of requiring the taking and processing of a pair of pictures instead of one. The extra space required by the incorporation of stereo pairs in plates for publication, however, cannot closely be estimated because of the presence of several variables, namely, the number and the spacing of stereograms and their combination with conventional photos.

By no means every view would warrant stereophotography. Careful selection of those views which would show most by stereophotography would cut down on the number needed. Where several specimens of the same species were to be illustrated one stereo pair should suffice unless particular details were to be emphasized.

In certain instances stereophotography might permit the elimination of views from other angles which would ordinarily be necessary. However, it is the firm belief of the writer that a stereogram is not and should not be used as an "all-in-one" view. It should be remembered that even though the apparent form seen in a stereogram is three dimensional, each image of the stereo pair is still a projection onto the plane of the photographic plate, and so actual dimensions and angular relations remain distorted and cannot be measured except where parallel to the plate.

In regard to quality of photographs it is worth remarking that where detail does not exist because of something less than perfect photographs, or where detail is subsequently lost as a result of the method of reproduction, the contrast between conventional and stereoscopic photographs is remarkable indeed. This can be demonstrated amply by examining any of the half-tone reproductions of stereograms which have appeared in texts, first viewing the elements singly as conventional photographs, and then stereoscopically.

Careful planning of plate layout would permit the greatest economy of space where stereograms are to be used. Plate 88 is designed to indicate several possible combintions of stereograms with conventional photos and with other stereograms, as well as to present sample stereo-illustrations of several different types of fossils. In the first and last horizontal rows, a stereogram is combined with two single photos. The second and fourth rows consist of two stereograms each, with the elements placed alternately. The fifth row is arranged similarly but with three stereograms instead of two. In the third row two small conventional

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EXPLANATION OF PLATE 88

The stereograms are numbered in sequence with the rest of the figures. An "s" after a figure number indicates that it is the right-hand element of a stereogram, the left-hand one bearing the same number. In all the stereograms the left-hand element has been taken with the plate vertically above the specimen. The right-hand element is slightly oblique. The angle between the two camera positions was in all cases 7 degrees. This produces an apparent convexity as seen with a stereoscope which compares closely to the actual convexity of the specimens. All specimens were coated with magnesium oxide. No photographs have been retouched.

FIGS. *1–1s, 2, 4–4s—Cryptolithus tesselatus* Green, silicified cranidium, ×5. *1–1s*, dorsal stereogram; *2*, side view; *4–4s*, ventral stereogram.

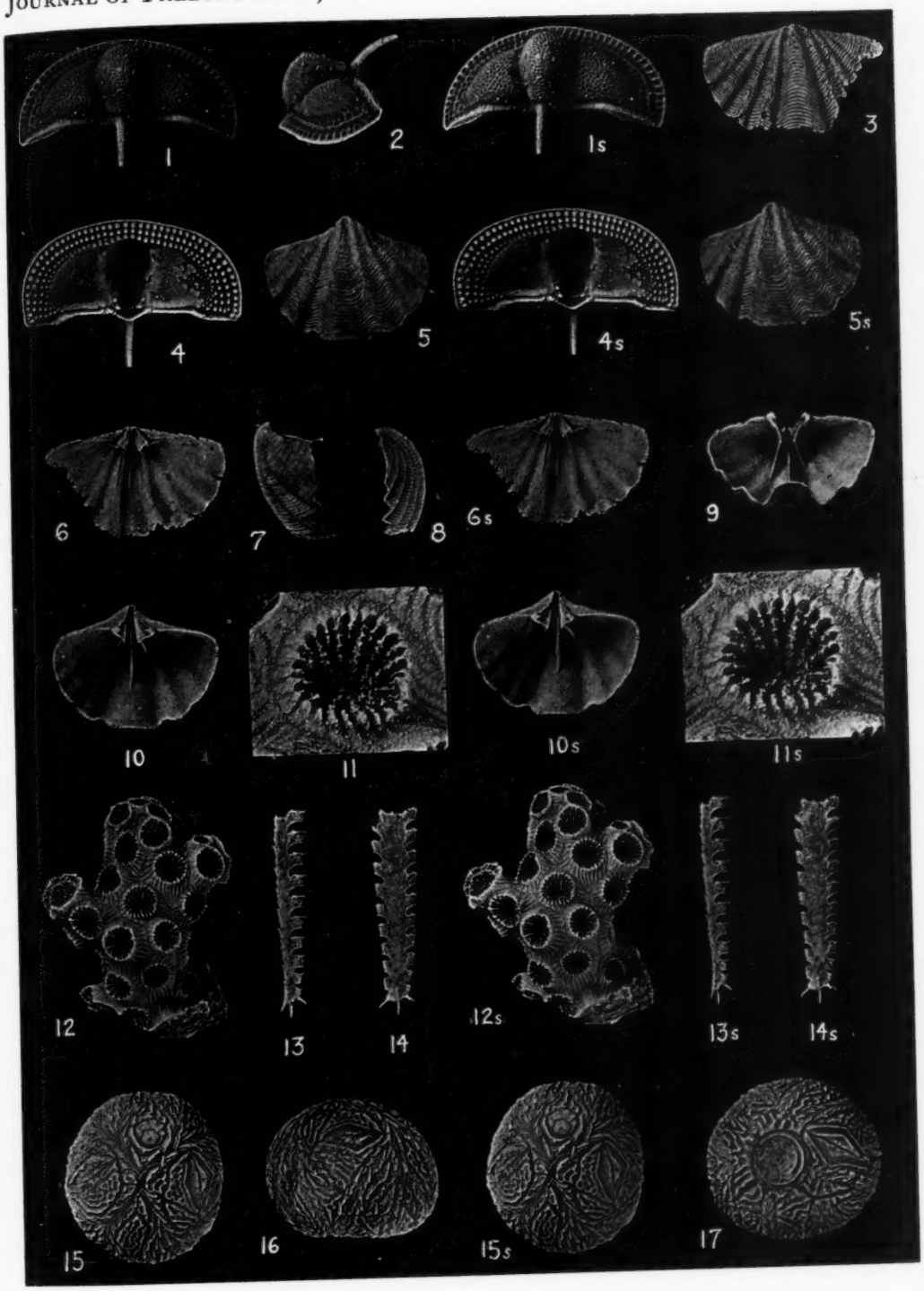
3, 6–6s, 8—Delthyris sp., silicified dorsal valve, ×2.3. *3*, exterior; *6–6s*, stereogram of interior; *8*, side view.

5, 5s, 7, 9, 10–10s—Delthyris sp., silicified ventral valve, ×2.3. *5, 5s*, stereogram of exterior; *7*, side view; *9*, interior seen from an antero-dorsal position; *10–10s*, stereogram of interior.

11–11s, 12–12s—Astrhelia palmata (Goldfuss). *11–11s*, stereo-detail of a single calyx, ×5; *12–12s*, stereogram of a small corallum, ×1.4.

13–13s, 14–14s—Climacograptus sp., ×5. Two stereograms of an uncrushed specimen etched free of its original matrix.

15–15s, 16, 17—Sphaerocystites multifasciatus Hall, ×1.4. *15–15s*, stereogram of top view; *16*, side view; *17*, basal view.



Evitt, Stereophotography

photos are set between the elements of a stereogram and a third single photo lies to the right.

In connection with plate layout it should be noted that although the distance between the two elements of a stereo pair is not a critical one, it would seem advisable to accept and adhere to some standard spacing, certainly for any one plate. For viewing with a small stereoscope this distance should be in the range of from 2 to 3 inches. The writer considers 2½ inches to be satisfactory. This permits easy viewing with a pocket stereoscope and at the same time is not too great for comfortable vision with the unaided eyes. This spacing also allows two stereograms of moderate size (or three smaller ones) to be placed in the same horizontal row on a plate which is 5 inches (±) wide. The three inch distance (advocated by Gott, 1945, p. 395) is a little too great for most individuals to view with the unaided eyes without eye strain. The considerably greater distance employed by Hudson permits the use of a correspondingly larger image. However, it is impossible to view such mounts without an optical instrument. This instrument must be larger and of slightly different design than that suitable for the closer spacing. Also the appreciable increase in plate space requirements demanded by the more remote spacing of larger images would seem disproportionate to the advantage gained.

STEREOPHOTOGRAPHS FOR PURPOSES OTHER THAN PUBLICATION

The importance of the only significant argument against the wide use of stereophotography—extra space requirements—disappears when we examine its potential uses for purposes other than publication. For record, reference, and teaching, stereophotography possesses especial possibilities worthy of mention.

Mounting of stereo pairs on standard 3″×5″ or 5″×8″ index cards would permit convenient filing. It would be possible for each worker in a field to amass a file of stereophotographs of type and comparative material with which he might be concerned. These photographs, possessing almost all the attributes of the actual specimens, would in most cases substitute satisfactorily for repeated study of the types and so protect these from the risks of transportation and handling. This would be particularly important in the case of especially rare or delicate specimens. It is pertinent to note that in their introduction Branson, Mehl and Branson (1933, pp. 16–17) state, with reference to conodonts: " . . . we have found that stereoscopic illustrations are equal or superior to the study of specimens under the binocular microscope. These stereoscopic views give a magnification difficult to obtain with the microscope without cutting down the light to the point of eye strain." Hudson (1913, p. 116) suggests the use of stereograms to construct models of destroyed specimens.

It is frequently necessary, either for photography or examination, to coat specimens with some whitening medium before details of ornamentation or structure become apparent, even under the microscope. Commonly ammonium chloride or magnesium oxide have been used as whitening agents. The first is only a temporary coating in a generally humid climate. The second is more stable, but neither is tolerant of surface abrasion of any sort. Thus, both have the shortcoming of requiring re-application for repeated study. Stereophotographs of whitened specimens once made, however, would not only be a permanent record but would preserve, ever ready for easy reference, the finest details of the subjects taken.

As a teaching aid in paleontology stereophotography should prove of considerable value. Copies of stereograms, mounted ready for viewing, could be easily reproduced in quantity in any photographic darkroom. These would permit careful study at appropriate magnifications of pre-selected and pre-oriented entire specimens, or details of specimens, on repeated occasions by large numbers of students simultaneously. Where microscopes are few stereograms would permit an economy in time in the study of microscopic details by large classes, and would permit an entire class to follow a single explanation by the instructor.

SUMMARY

The practicability of the extensive use of stereophotography for purposes of publication will depend on the outcome of a careful

weighing of the extra expense involved versus the benefits derived there from as discussed above. It seems to the writer, however, that only general inertia can long oppose the adoption of its use in other ways as an additional tool of the paleontologist. Time should see the day when the stereoscope becomes as common a fixture of the paleontologic laboratory as the microscope, and when stereophotography will be the usual practice rather than the subject of periodic advertisement.

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MANUSCRIPT RECEIVED FEBRUARY 1, 1949.

JOURNAL OF PALEONTOLOGY, VOL. 23, NO. 5, PP. 571–572, SEPTEMBER 1949

PALEONTOLOGICAL NOTES

FOOTNOTES TO *EOBRONTEUS*

G. WINSTON SINCLAIR
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Dr. H. B. Whittington has kindly drawn my attention to two points in my paper on this genus (Sinclair 1949) which require correction or comment.

Firstly, my citation of Kildare as the locality of *Eobronteus hibernicus* (Portlock) (p. 53), was quite wrong. The species was described from beds along the Tirnaskea river in Desertcreat Parish, County Tyrone.

Secondly, Whittington questions my reference of the Craighead limestone at Girvan to the Upper Ordovician. In this I was following Reed, whose opinion I accepted because of his wide first-hand experience with the Girvan faunas. However, there is little agreement about the age of these beds, and it might be well to summarize some of the more recent opinions, which may be unfamiliar to American students.

Until recently most workers have followed Lapworth, who (1882, p. 580 seq.) described the limestones seen in the Craighead quarries, as "Stinchar Limestone." This unit he had described from exposures along the Stinchar River (p. 555), which is only about eleven miles from Craighead, but the structure of the region is highly complex, and no direct correlation can be made. The horizon of the Craighead fossils is given as Stinchar in some early papers on the Girvan faunas, but usually the locality permits separation of the one from the other. In his monograph on the pelecypods Hind (1910) gives the horizon of the Craighead species only as "Llandeilo."

It was later realized that the faunas of the Stinchar and the Craighead were distinct, but some workers have kept the latter as a unit of the Stinchar Limestone Group. This is the course followed by Pringle (1935, p. 24) who puts the Stinchar Group in the Barr Series (following Lapworth), and refers it to the Lower Caradocian. Jones also (1935, p. 9) apparently retains the Craighead in the Stinchar Group, and refers it to the Lower Bala [Caradocian].

Lamont (1934, p. 163) considers the Craighead to equal the Upper Stinchar, or to be immediately post-Stinchar in age, and thus (Lamont 1935, p. 290) Lower Caradocian.

Stubblefield (1939, p. 59) makes no precise correlation, but states that the graptolite fauna of the Craighead "would seem to indicate that the age of the limestone is later than Stinchar."

Anderson & Pringle (1946, p. 175) consider the Craighead to be a reef facies of the Balclatchie, and thus still Caradocian, but somewhat younger than the Stinchar.

Ulrich (1930, p. 85) recognized the strong Balclatchie aspect of the Craighead fauna, but considered the "Balclatchie" species to be survivors into a much later time. He correlated the Craighead with the Drummuck, as a calcareous facies, and thus Ashgillian in age. In terms of the American sequence he (table, p. 73) placed these beds as Richmondian or Alexandrian.

Reed (1935) discussed the Craighead fauna in detail, but stated only his opinion that it was of "Upper Ordovician" age. However, it is clear from the paper that by this he meant Ashgillian, as he refers frequently to the similarities between the Craighead and the Keisley and Kildare beds, which he correlated with the Drummuck.

Thus we have recent competent British workers referring the Craighead to various positions in the Caradocian, and to the Ashgillian. Until those immediately concerned with the beds can agree on their age it is difficult for a foreign student to choose between them. He can, however, refrain from tagging them "Upper Ordovician" without comment, and I should have done so.

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PROSOPON, A TERM PROPOSED TO REPLACE THE BIOLOGICALLY ERRONEOUS TERM *ORNAMENT*

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While describing fossil brachiopods, trilobites, and other organisms, one has had constantly to employ the terms *ornament* and *ornamentation*, but with a rapidly growing sense of dissatisfaction! There is no such thing as ornament from the biological point of view. The so-called ornament is an organ, a structure with a function. For example, it has been suggested that the rugae of *Leptaena* were of value in holding it in place on the sea-floor, and that the costellae of *Chonetes* were associated with setae which kept foreign bodies from the mantle cavity as they do in some extant brachiopods.

Objection is taken to the term *ornament* because:

1. It has all the disadvantages of a word taken over from everyday speech. Its connotation is too wide; it is not definitive enough for scientific purposes.
2. The term gives an erroneous impression of something merely decorative, of something additional to essentials. But these external structures are organs of real biological significance. They are genetically maintained, as is shown by their constancy in a species and their continuance through an evolutionary sequence. Besides being persistent in time, these structures are often also physiologically expensive, and so would be discarded by natural selection if they were not of biological value.

It appears that some general scientific term is required to refer to the exterior aspect, the surface character of the exoskeleton of the mollusc, trilobite, or other organism being described. *PROSOPON*, the Greek word for *face*, suggests itself as being appropriate. If desired, a verb can be formed by adding the Greek ending *-ise*. It is proposed therefore that *prosopon* be an over-all term for the description of surface appearance, and it is envisaged that as palaeobiological knowledge increases, a number of subsidiary terms will emerge for structures of different functions.

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NOMENCLATURAL NOTES

A NEW NAME FOR *CARINORBIS* YEN

TENG-CHIEN YEN

Recent checking of generic names reveals that *Carinorbis* Yen (Amer. Jour. Sci. 244 (1), p. 46, 1946) is preoccupied by Conrad 1862 (Proc. Acad. Nat. Sci. Phila., 14, p. 288) for some Miocene species of marine gastropods. Conrad suggested (Amer. Jour. Conch., 2, p. 100, 1866) that his genus is related to *Lysis* Gabb, while Dall (Trans. Wagner Inst. Philadelphia, 3, p. 322, pl. 18, fig. 3a, 1892) considered it to be a synonym of *Fossarus* Philippi. However, the validity of Conrad's name necessitates the substitution of *CARINULORBIS*, new name, for *Carinorbis* Yen 1946, with *C. planospiralis* Yen as its genotype.

ONISCOIDICHNUS, NEW NAME FOR *ISOPODICHNUS* BRADY 1947 NOT BORNEMANN 1889

L. F. BRADY
Museum of Northern Arizona, Flagstaff

The generic name *Isopodichnus* was proposed by me in this journal (Jour. Paleontology, vol. 21, 1947, p. 470) for an invertebrate track in the Coconino sandstone. My attention has been called by Dr. Otto Haas to the prior use of this name by Bornemann in 1889 for a track in the Buntsandstein. Bornemann's material was described in more detail by Schindewolf (Senckenbergiana, vol. 10, 1928, pp. 27 seq.), but although the generic name was retained, no comparison was made with similar tracks of any specific kind of isopod, nor indeed was any clear reason adduced for referring the track to an isopod.

While the reference of almost any invertebrate track to a definite life form or even to a particular class is apt to be very uncertain, in spite of possible resemblance to a Recent print of known origin it does not seem reasonable to use the same generic name for a terrestrial Permian track and for the form described by Bornemann and Schindewolf from a lagoonal or marine environment of Triassic age. I therefore propose for the Coconino sandstone form the generic name *Oniscoidichnus* (genotype: *Isopodichnus filiciformis* Brady 1947). The name is given because of the resemblance to the Recent track made in a similar sand dune environment by *Oniscus* and other oniscoid isopods.

POSSIBILITY OF SYNONYMOUS HOMONYMS

OTTO HAAS
The American Museum of Natural History, New York

The case dealt with in the preceding note is bound to arouse particular nomenclatural interest since it proves the possibility of synonymous homonyms.

For both Bornemann in 1889 and Brady in 1947 proposed, *independently*, the same generic name for what both considered to be isopod tracks. Thus, *Isopodichnus* Bornemann and *Isopodichnus* Brady are clearly homonyms. Had the tracks studied by both authors proved to be attributable to the same (otherwise unknown) genus, then *Isopodichnus* Brady would, in addition to being a homonym of *Isopodichnus* Bornemann, be also a synonym of that earlier name.

Since, however, Mr. Brady arrives in the preceding note at the conclusion that his Permian tracks should not be considered congeneric with Bornemann's and Schindewolf's Triassic ones, both names are homonyms but not also synonyms. Still, the present case proves at least the theoretical possibility, under particular conditions, of synonymous homonyms (or homonymous synonyms, for that matter).

JOURNAL OF PALEONTOLOGY, VOL. 23, NO. 5, P. 575, SEPTEMBER 1949

NOMINATIONS FOR MEMBERSHIP

In accordance with Article 3, Chapter 1 of the By-Laws of the Society the Secretary submits the following names of applicants for election to membership for consideration by the Members of the Paleontological Society.

BUSH, JAMES, 2095 Union St., Brooklyn, New York; A.B., 1941, New York Univ., Graduate Student, New York Univ., but will return to former position as Instructor, Invertebrate Paleontology and Micropaleontology, Univ. of Miami, Fla. Proposed by J. J. Galloway, Brooks F. Ellis, B. F. Howell.

CORMACK, WALTER BERNARD, Dept. of Geology, The Johns Hopkins Univ., Baltimore 18, Md. B.S., 1939, Univ. of South Carolina. Graduate student, The Johns Hopkins Univ. Interested in invertebrate paleontology. Proposed by H. E. Vokes and Donald A. Myers.

HUGHES, EMILY MARY, Michigan Geological Survey, East Lansing, Mich.; B.S., Mich. State Coll., Interested in micropaleontology, now working on microfauna of the Traverse Group. Proposed by G. M. Ehlers and William A. Kelly.

KJELLESVIG-WAERING, ERIK NORMAN, 415 Philtower Bldg., Tulsa, Okla. B.S., 1934, Univ. of North Carolina. Chief Geologist, Helmerick and Payne, Inc. Interested in invertebrate paleontology, especially fusulinids and Eurypterida. Proposed by Kenneth E. Caster, G. Arthur Cooper and B. F. Howell.

MANDRA, YORK T., 1729 Oxford Street, Berkeley, Calif. A.B., 1948, Univ. of California. Graduate student and Museum technician, Univ. of California. Interested in micropaleontology. Proposed by J. Wyatt Durham, R. A. Stirton, and R. M. Kleinpell.

WILSON, DRUID, Frostproof, Fla. B.S., 1929, Southern College, Lakeland, Fla. Citrus grower and amateur paleontologist. Interested in Tertiary invertebrata. Proposed by Katherine V. W. Palmer and G. D. Harris.

WILSON, EUGENE JACK, Dept. of Paleontology, Univ. of California, Berkeley 4, Calif. A.A., Mesa College, Colorado; A.B., Univ. of California; Graduate Student, Univ. of California. Interested in micropaleontology. Proposed by J. Wyatt Durham, R. M. Kleinpell, and R. A. Stirton.

WRIGHT, LEO M., Swallow Hall, Univ. of Missouri, Columbia, Mo. B.S., M.S., Univ. of Tulsa. Graduate Student and Assistant Instructor of Geology, Univ. of Missouri. Interested in micropaleontology. Proposed by Raymond E. Peck and A. G. Unklesbay.

YOUNG, BERNICE, Dept. of Paleontology, Univ. of California, Berkeley 4, Calif. A.B., 1948, Univ. of California. Graduate Student and Museum Technician, Univ. of California. Interested in micropaleontology. Proposed by J. Wyatt Durham, R. M. Kleinpell, and R. A. Stirton.

JOURNAL OF PALEONTOLOGY, VOL. 23, NO. 5, P. 576, SEPTEMBER 1949

REVIEW

LOWER ORDOVICIAN OSTRACODS OF THE SILJAN DISTRICT, SWEDEN, by Ivar Hessland. Bull. Geol. Institute Upsala, vol. 33, pp. 97–408, 18 pls., 8 charts, 1949.

Lower Ordovician ostracode faunules have seldom been thoroughly investigated, so this well-documented work deserves wide notice. On fragments of the thoroughly lithified *Orthoceras* limestone (Chazyan) the author collected and prepared about 5300 specimens. This task was but part of a systematic investigation of all features of the Ordovician beds of the Siljan District, and as a result more than usual information is given on the paleoecology and mineralogy of the enclosing sediments.

Hessland follows Triebel's 1941 conclusion that the central adductor muscle group scars lie to the anterior of the midpoint of the shell, and adds convincing evidence in support of this determination. Brood pouches of various types are discussed at length, and the author concludes that they may not all have served the purpose of brooding eggs or larvae.

With large numbers of individuals available for study the author has been able to present important data on larval features, growth stages and sex dimorphism.

About 700 specimens were measured during the study, seven measurements being made on each individual. These results are tabulated, together with calculated ratios, as evidence used in the present study and available for further statistical investigation.

Eighty species of ostracodes, 73 of them named, have been recognized by Hessland in this faunule. New forms are assigned as follows: APARCHITIDAE—*Conchoides* n. gen. (type *C. micropunctata* nov.) and eight other species; *Aparchites* (3); *Macronotella* (3); *Ceratocypris* (1); *Pinnatulites* n. gen. (type *Primitiella procera* Kummerow 1924) and two other species. PRIMITIIDAE—*Primitiella* (4); *Ectoprimitia* (1); *Haploprimitia* (1); *Laccoprimitia* (2); *Conchoprimites* n. gen. (type *C. reticulifera* nov.). HOLLINIDAE—Hessland credits this family to Schmidt 1941 rather than to Swartz 1936, recognizes the four subfamilies used by Schmidt (Hollininae, Ctenentominae, Tetradellinae and Ctenonotellinae) and adds the subfamilies Eurychilininae Ulrich and Bassler and Euprimitiinae nov. Included in the family are *Euprimitia* (3); *Euprimites* n. gen. (type *E. reticulogranulata* nov.); *Eurychilina* (2); *Laccochilina* n. gen. (type *Eurychilina estonula* Öpik 1935) and four other species; *Ctenentoma* (5); *Aulacopsis* n. gen. (type *A. bifissurata* nov.) and two other species; *Glossopsis* n. gen. (type *G. lingua* nov.) and nine other species; *Ogmoopsis* n. gen. (type *O. nodulifera* nov.) and one other species; *Ceratopsis* (1); *Tetradella* (2); *Steusloffia* (1). KLOEDENELLIDAE—*Kloedenella* ? (1). CYPRIDAE—*Bythocypris* (7).

A. S. WARTHIN

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